⑫

**US Army Corps
of Engineers**

AD-A187 398

GRAVEL BAR MUSSEL COMMUNITIES:
A COMMUNITY MODEL

by

Andew C. Miller, Barry S. Payne,
Teresa J. Naimo

Environmental Laboratory

DEPARTMENT OF THE ARMY
Waterways Experiment Station, Corps of Engineers
PO Box 631, Vicksburg, Mississippi 39180-0631

and

W. D. Russell-Hunter

Syracuse University
Syracuse, New York 13210

DTIC
ELECTE
NOV 2 5 1987
S   D

October 1987
Final Report

Approved For Public Release Distribution Unlimited

87 11 13 051

REPORT DOCUMENTATION PAGE

1a REPORT SECURITY CLASSIFICATION	1b RESTRICTIVE MARKINGS
Unclassified	

2a SECURITY CLASSIFICATION AUTHORITY	3 DISTRIBUTION/AVAILABILITY OF REPORT
2b DECLASSIFICATION/DOWNGRADING SCHEDULE	Approved for public release; distribution unlimited

4 PERFORMING ORGANIZATION REPORT NUMBER(S)	5 MONITORING ORGANIZATION REPORT NUMBER(S)
Technical Report EL-87-13	

6a. NAME OF PERFORMING ORGANIZATION	6b OFFICE SYMBOL (If applicable)	7a NAME OF MONITORING ORGANIZATION
USAEWES, Environmental Laboratory; Syracuse University	WESER-A	

6c. ADDRESS (City, State, and ZIP Code)	7b ADDRESS (City, State, and ZIP Code)
PO Box 631, Vicksburg, MS 39180-0631; Syracuse, NY 13210	

8a. NAME OF FUNDING/SPONSORING ORGANIZATION	8b OFFICE SYMBOL (If applicable)	9 PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER
US Army Corps of Engineers		

8c. ADDRESS (City, State, and ZIP Code)	10 SOURCE OF FUNDING NUMBERS			
	PROGRAM ELEMENT NO	PROJECT NO	TASK NO	WORK UNIT ACCESSION NO
Washington, DC 20314-1000				EIRP 32390

11 TITLE (Include Security Classification)

Gravel Bar Mussel Communities: A Community Model

12 PERSONAL AUTHOR(S)
Miller, Andrew C.; Payne, Barry S.; Naimo, Teresa J.; and Russell-Hunter, W. D.

13a. TYPE OF REPORT	13b TIME COVERED	14 DATE OF REPORT (Year, Month, Day)	15 PAGE COUNT
Final report	FROM _____ TO _____	October 1987	71

16. SUPPLEMENTARY NOTATION
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161

17 COSATI CODES			18 SUBJECT TERMS (Continue on reverse if necessary and identify by block number)
FIELD	GROUP	SUB-GROUP	Aquatic habitat Habitat evaluation
			Ecology Impact assessment
			Freshwater mussels

19 ABSTRACT (Continue on reverse if necessary and identify by block number)

Literature and field data were synthesized to prepare a community model for thick-shelled unionid mussels (*Quadrula, Amblema, Plectomerus, Megalonaias, Obovaria,* and *Obliquaria*, etc.) that are found in gravel substrate in medium- to large-sized rivers. This model, developed for use with the Habitat Evaluation Procedures of the US Fish and Wildlife Service, can be used for general planning purposes, and to gain a more complete understanding of the biology and ecology of thick-shelled freshwater mussels. The distribution of these species, with respect to the following physical and chemical variables, is reviewed: water velocity, particle type, sediment stability, deposited sediment retained annually, minimum depth, maximum sustained water temperature, minimum sustained dissolved oxygen, and calcium hardness. Physical, chemical, and biological characteristics of large river systems where these organisms are found are reviewed. The biology and

(Continued)

20 DISTRIBUTION/AVAILABILITY OF ABSTRACT	21 ABSTRACT SECURITY CLASSIFICATION
☑ UNCLASSIFIED/UNLIMITED ☐ SAME AS RPT ☐ DTIC USERS	Unclassified

22a NAME OF RESPONSIBLE INDIVIDUAL	22b TELEPHONE (Include Area Code)	22c OFFICE SYMBOL

DD Form 1473, JUN 86   Previous editions are obsolete   SECURITY CLASSIFICATION OF THIS PAGE

19.   ABSTRACT (Continued).

ecology of freshwater mussels, including feeding, locomotion, behavior, reproduction, and early development, are discussed.

PREFACE

In 1980, the Office of the Chief of Engineers (OCE), US Army, funded a 2-year program on freshwater molluscs at the US Army Engineer Waterways Experiment Station (WES) through the Environmental Impact Research Program (EIRP), Work Unit 32390. Following completion of that work, plans were made to prepare a community model for freshwater mussels (family Unionidae) that live in gravel bars in large rivers. With funds from the US Army Engineer Districts of Louisville, Nashville, and Mobile, as well as EIRP, quantitative data were obtained from mussel beds in large rivers. The model described in this report is based upon those studies.

This report was prepared by Dr. Andrew C. Miller, Dr. Barry S. Payne, and Ms. Teresa J. Naimo of the Aquatic Habitat Group (AHG), Environmental Resources Division (ERD), Environmental Laboratory (EL), WES. Dr. W. D. Russell-Hunter, Syracuse University, Syracuse, N. Y., prepared Part III of this report and assisted in preparation of the Suitability Index curves. The report was edited by Ms. Marsha Gay of the WES Information Products Division, Information Technology Laboratory.

Studies on freshwater molluscs at WES are under the general supervision of Dr. Thomas D. Wright, Chief, AHG; Dr. Conrad J. Kirby, Chief, ERD; and Dr. John Harrison, Chief, EL. Dr. Roger T. Saucier is WES Program Manager of EIRP. The Technical Monitors for the EIRP are Dr. John Bushman and Mr. Earl Eiker, OCE, and Mr. Dave Mathis, Water Resources Support Center.

COL Dwayne G. Lee, CE, was the Commander and Director of WES. Dr. Robert W. Whalin was Technical Director.

1

CONTENTS

CONVERSION FACTORS, NON-SI TO SI (METRIC)
UNITS OF MEASUREMENT

Non-SI units of measurement used in this report can be converted to
SI (metric) units as follows:

Multiply	By	To Obtain
atmospheres (standard)	101.325	kilopascals
cubic feet	0.02831685	cubic metres
cubic yards	0.7645549	cubic metres
feet	0.3048	metres
miles (US statute)	1.609347	kilometres
tons (2,000 pounds, mass)	907.1847	kilograms

GRAVEL BAR MUSSEL COMMUNITIES: A COMMUNITY MODEL

PART I: INTRODUCTION

Background on Mussels

1. Freshwater mussels are a unique resource with economic, cultural, and ecological value. In this country their meat has been used for food, and the shells used to make ornaments, tools, and pearl buttons. Presently, shells are collected and shipped to the Orient where they are processed into inserts for the cultured pearl industry. Because they are long lived and practically nonmotile, their presence at a site provides evidence of previous habitat conditions. There are over 200 species of freshwater mussels in this country; of these, 28 are on the list of Endangered Species and are protected by the Endangered Species Act.

2. Freshwater mussels can be collected in ponds, lakes, streams, and large rivers. When present, they often dominate the benthic fauna, both in numbers and biomass. They can be found in a variety of substrates including mud, silt, sand, and gravel, or between and under large rocks. However, they are most likely to be found in a mixture of sand, gravel, and mud in large rivers of the central United States. A gravel bar habitat can support from 15 to more than 25 species; densities can exceed 100 per square metre.

Habitat-Based Evaluation Methods

3. In the 1970s the US Fish and Wildlife Service began development of the Habitat Evaluation Procedures (HEP) for use in impact assessment and habitat management. The HEP is an accounting system that enables a user to rate the value of habitat for organisms of interest. Central to the HEP are Suitability Index (SI) curves, which quantify the response of an organism to physical variables such as depth, substrate type, or water velocity. These SI curves can be grouped into a Habitat Suitability Index (HSI) model. HSI models have been prepared for a variety of birds, mammals, fishes, and selected invertebrates and are available from the US Fish and Wildlife

Service. An HSI model is a complex hypothesis of species-habitat relation-
ships and is not a statement of proven cause and effect.

4. The HSI model described herein deals with mussel species that
inhabit gravel bars in large rivers. Literature and field data pertaining to
these mussels have been synthesized into a 0.0 to 1.0 index score that quan-
tifies the ability of habitat to provide necessary life requisites for these
organisms. Assumptions used to transform habitat use information into the
index scores are noted, and guidelines for application of the model are
described.

Purpose and Scope

5. The purpose of this report is to describe an HSI model for thick-
shelled freshwater mussels that can be used for impact analysis, planning, and
resource management conducted by Federal, state, and private agencies. This
model is intended primarily for mussels in the following genera: *Quadrula*,
Amblema, *Plectomerus*, *Megalonaias*, *Obliquaria*, and *Obovaria*.

Hydrology

6. Although there are over 3.25 million miles* of streams in the
48 contiguous states, large rivers dominate the landscape (Figure 1). Flowing
water or lotic systems are characterized by unstable bottoms, high turbidity,
high dissolved oxygen, meandering channels, and unidirectional, occasionally
turbulent flow. Of the 76 cm of rainfall received by this country annually,
approximately 23 cm contribute to the flow of rivers (Figure 2).
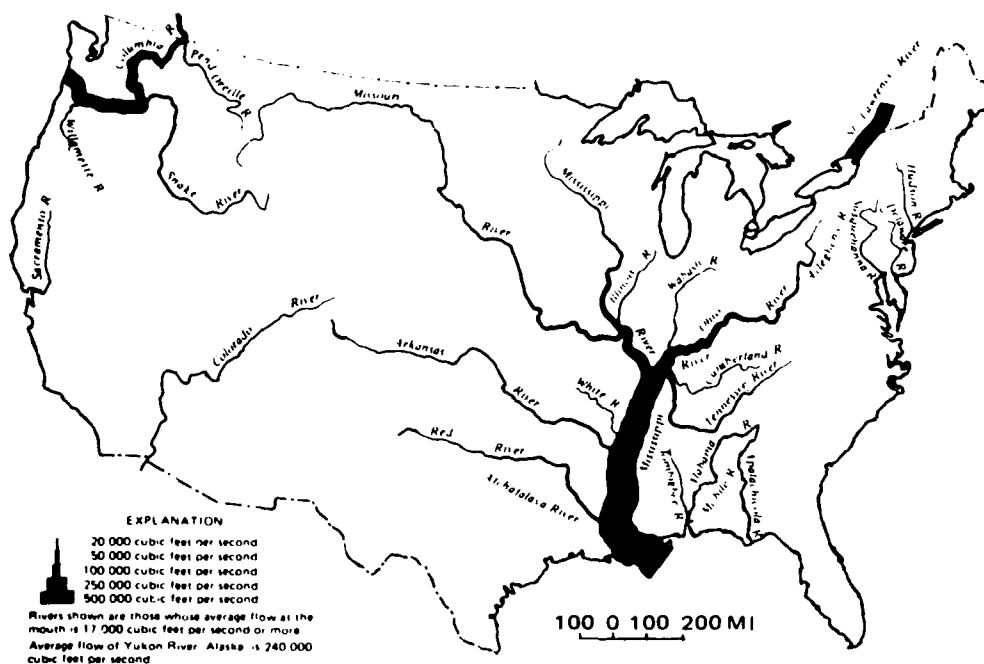
Figure 1. Major rivers in the United States based on discharge
(from Geraghty et al. 1973)

7. Lotic systems can be categorized based upon the following three
factors: flow, drainage pattern, and order. Flow can be ephemeral and occur
after storms, or intermittent and exist only during the wet season. Most
streams are perennial and persist throughout the year. Drainage pattern is
dependent upon geomorphology: dendritic types are in flatlands, rectangular
types are typical of faulted areas, and trellis types are found where there is

---

* A table of factors for converting non-SI to SI (metric) units of measure-
ment is found on page 4.
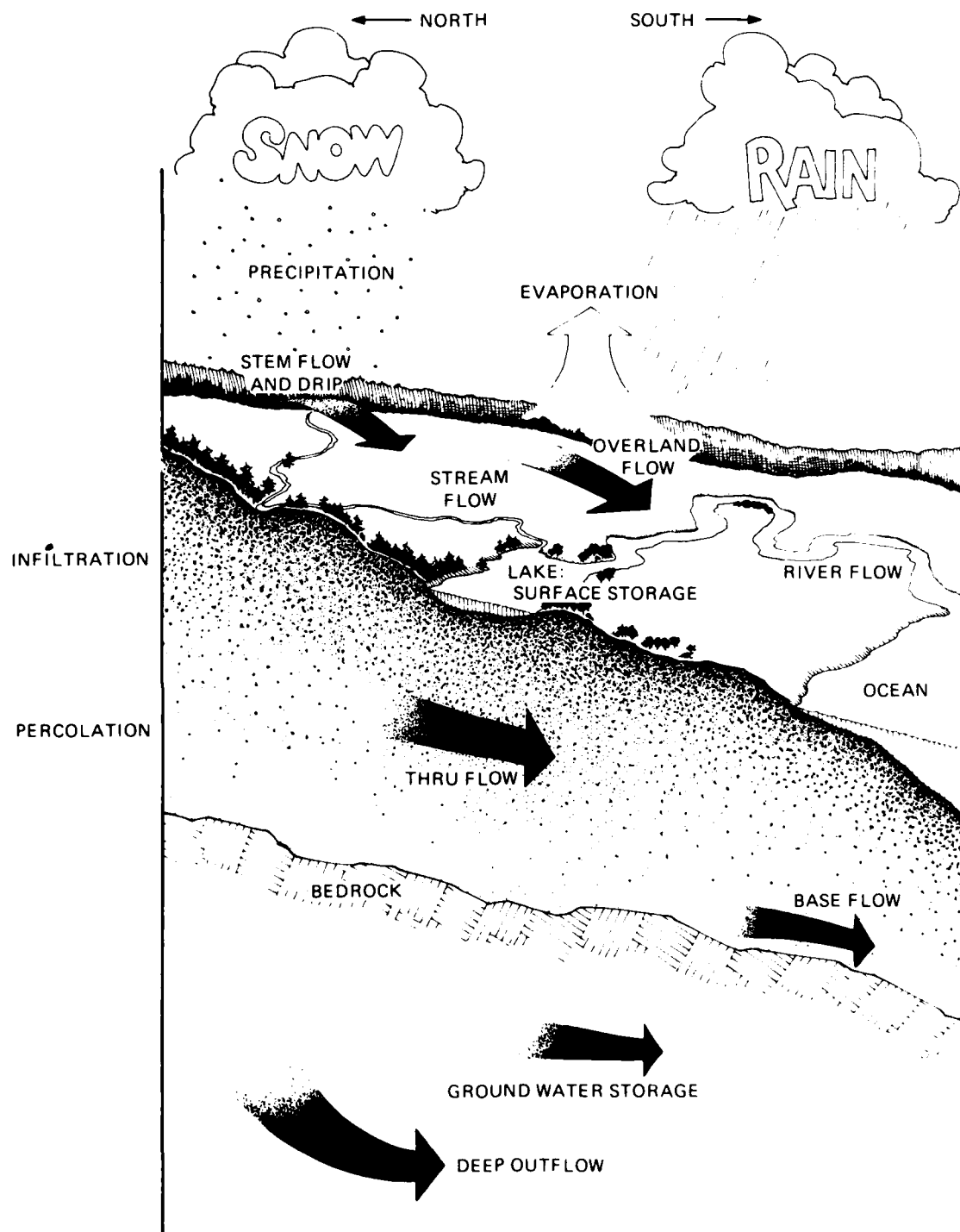
Figure 2. Hydrologic processes in rivers

folding of the strata (Figure 3). A stream ordering system was devised by Horton in 1945 as a means to differentiate waterways (Figure 4). A headwater stream has an order of 1; when two first-order systems join, they produce a second-order system. Order increases moving from headwaters to mouth; the highest river order is 12. Each order has its own unique physical and bio-logical characteristics. Of the 3.25 million miles of flowing water, 85 per-cent are first- and second-order streams. The lower Mississippi, Missouri, and Ohio Rivers are 12th-, 8th-, and 7th-order systems, respectively.

8. Velocity, an important hydrologic parameter, influences erosion rates, sediment transport, and distribution of aquatic organisms. In rivers velocities can range from near zero to more than 9 m/sec (Coker et al. 1921). In rivers with velocities greater than 30 cm/sec, aquatic insects, worms, and most other invertebrates seek shelter among rocks and other obstacles. In the boundary layer (1 to 3 mm) along the stream bottom where the current approaches zero (Figure 5), attached algae, immature insects, and mussels can exist because they are protected from high-velocity water. In large rivers, high water velocity can limit the presence of bivalves. In the midchannel of certain rivers, velocities exceed 60 cm/sec; such habitats are inimical to unionids.

9. Rivers have the ability to transport large quantities of material (or suspended load) in the water column (Reid and Wood 1976). The Mississippi River at Vicksburg carries approximately 1 million cu yd per day (Mathis et al. 1981). Livingstone (1963) calculated that the rivers of the world deliver 3.9 billion tons of dissolved material to the oceans annually. Although 10 constituents accounted for the majority of the dissolved material, calcium, bicarbonate, silicate, and sulfate predominated. Small streams are a source of particulate and dissolved organic material for the larger rivers. Leaves, twigs, and other vegetation are processed in small streams and exported downriver.

Erosion and Deposition

10. High velocity and maximum erosion in a river take place next to concave banks on the outside of bendways (Figure 6). In a straight reach the
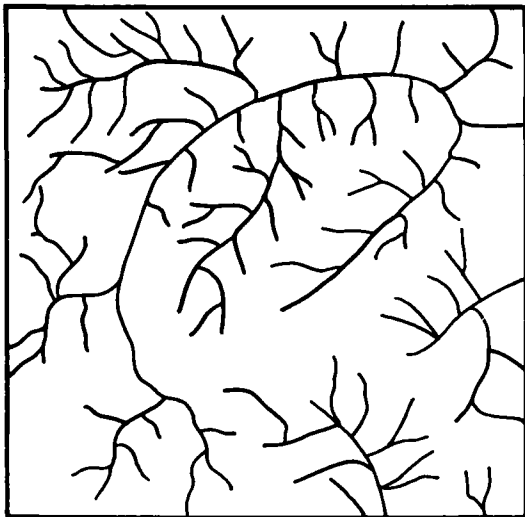
a. Dendritic
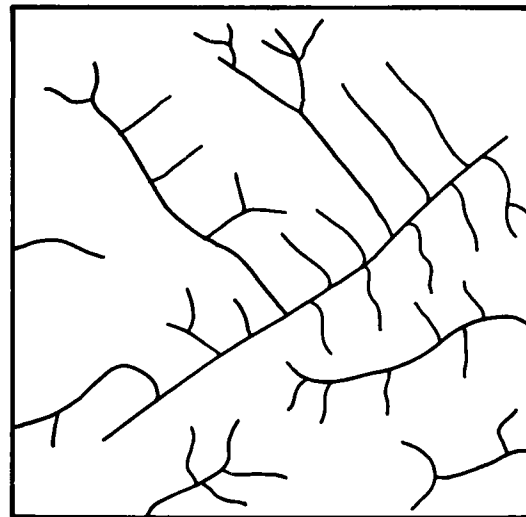
b. Rectangular
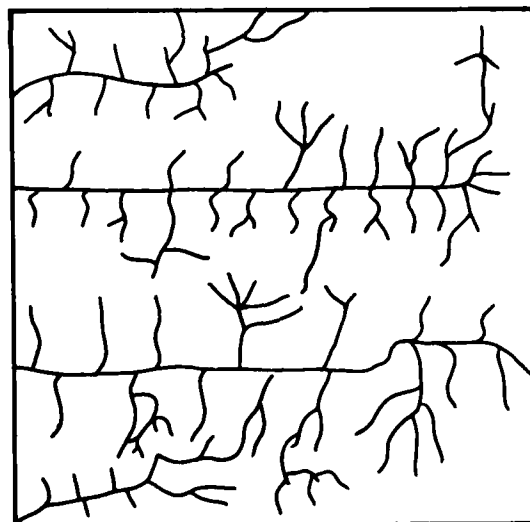
c. Trellis

Figure 3. Common drainage patterns
in flowing water systems
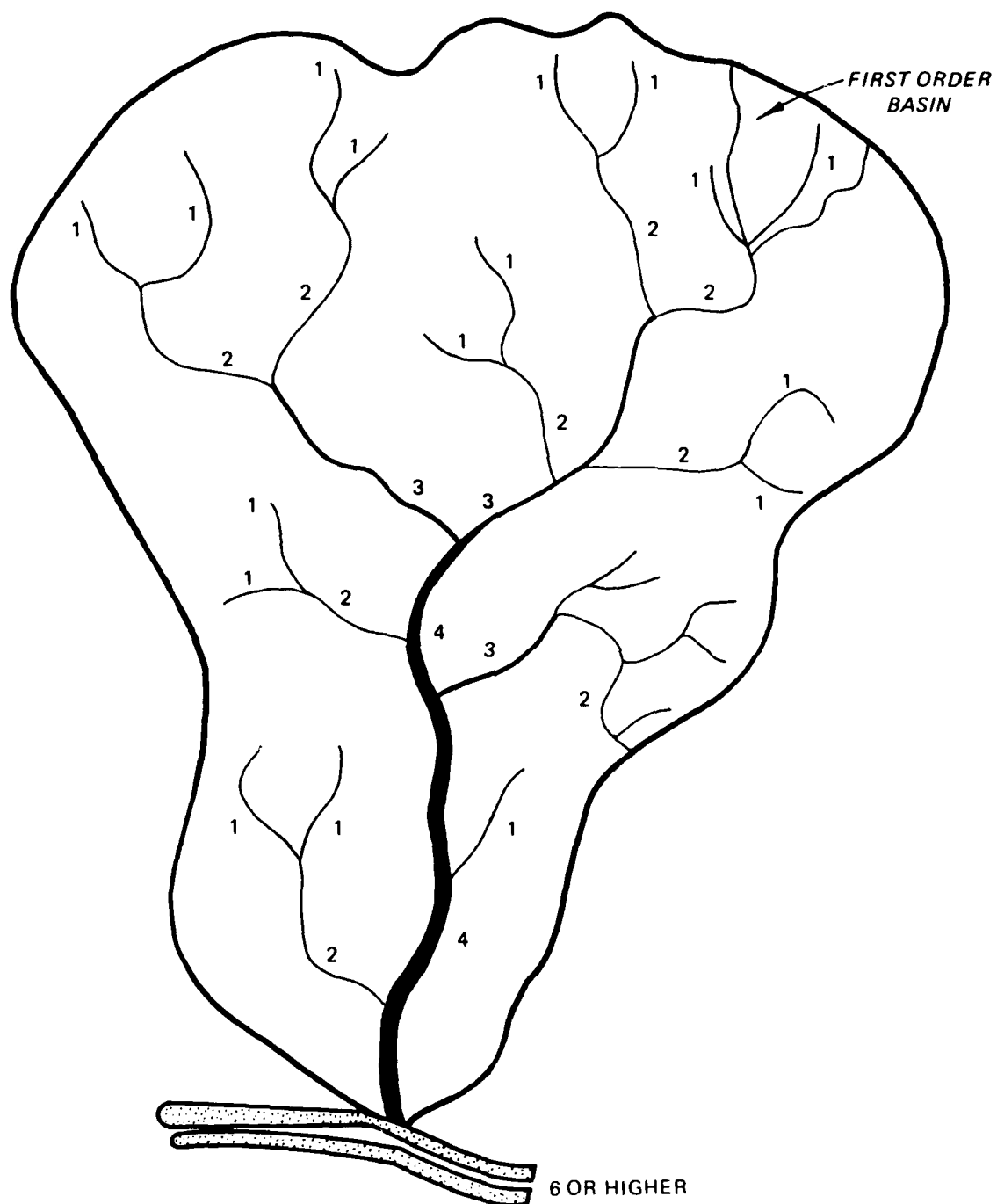
Figure 4. The stream ordering system
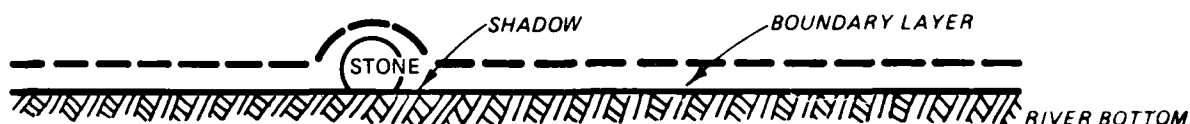
Figure 5.   The boundary layer in rivers
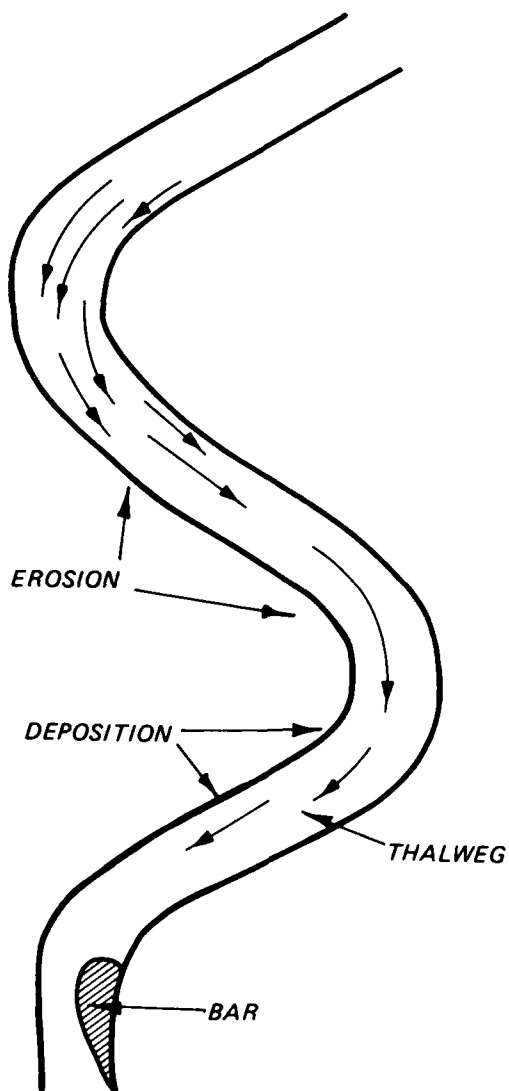
Figure 6.   Idealized flow pattern
of a large river (modified from
Leopold et al. 1984)

maximum velocity is often near the center (thalweg) and at approximately one-third the depth (Figure 7). An erosional zone or riffle is found where the substrate is scoured and the currents are usually greater than 30 cm/sec. Depositional zones, or pools, occur where currents are reduced and fine particles accumulate. A spate is a short period of high water caused by a

12
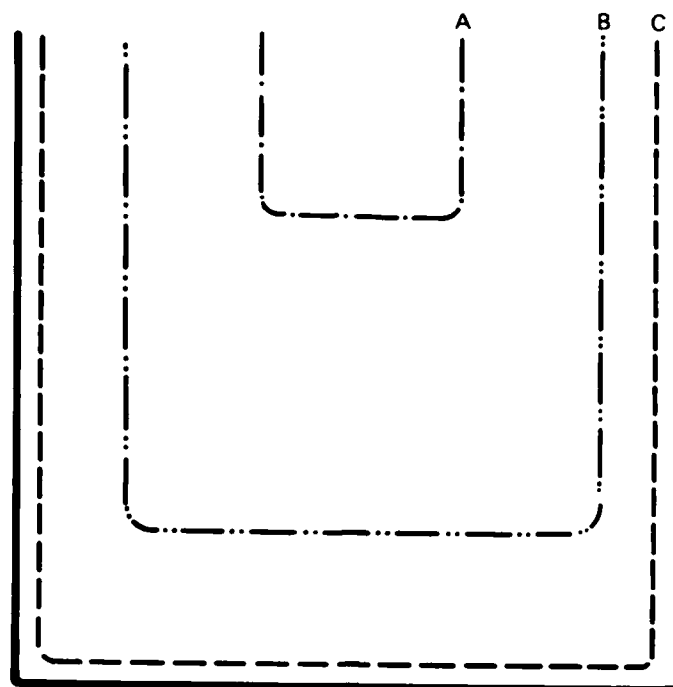
A = MAXIMUM FLOW AT 1/3 DEPTH AND CENTRALIZED
B = MEAN VELOCITY AT 6/10 DEPTH
C = MINIMUM   FLOW AT RIVER EDGES

Figure 7.   Velocity differences in stream
cross section

storm, which frequently erodes and reworks base material. After a flood, the
river will return to base flow although the time required depends on stream
size and intensity of the event.

11. In large river habitats, molluscs exist in both depositional and
erosional zones. In the St. Francis River, northern Arkansas, large numbers
of *Proptera capax* can be collected in depositional, straight reaches of the
river. The mussel beds in the Tombigbee, Ohio, Cumberland, and Upper
Mississippi rivers are in erosional zones. At these sites, however, current
velocities are usually less than 30 cm/sec and the substrate is stable. Coker
et al. (1921) discussed the cross-sectional distribution of mussels in a
river. It was determined that the nature of the substrate (i.e. erosional or
depositional), rather than the water depth, was most the important in deter-
mining the location of bivalves. Because bivalves live partially buried in
the substrate, they avoid the erosive action of high-velocity, sediment-laden

water. When molluscs are found in high-velocity sites, their shells can be heavily eroded.

Substrate

12. Substrate conditions depend on the nature of the surrounding terrain and on the size of the river (Reid and Wood 1976). In the lower reach of a river, the substrate is usually characterized by silt, mud, and detritus (Table 1). In the middle reaches, coarser materials are found, while in the upper reaches, large rocks and boulders predominate. In most rivers, mean particle size decreases in a downstream direction, and a correlation exists between particle size and slope (Hawkes 1975, Hynes 1970). Stream orders 1-3 have large-sized coarse materials, and orders 4-6 exhibit both coarse and fine materials. Fine materials predominate in orders greater than 7. Gravel bars in rivers are depositional sites that occur when velocity declines and coarse materials drop out of the water column (Figure 8). These habitats provide permanent, stable substrate for mussels.

Table 1

Major Differences Between Headwater and Large River Systems

Parameter	Headwater Streams	Large Rivers
Substratum	gravel rock	sand mud clay silt
Turbidity	low	high
Light penetration	moderate	low
Major invertebrate functional group	shredders, scrapers, and predators	collectors
Total dissolved solids	low	high
Canopy cover	high	low
Gradient	high	low
Suspended particulates	low	high
Dominant fish group	trout sculpin stonerollers	drum buffalo catfish

a. Natural gravel bar in the Tombigbee River near Aliceville, Ala.

b. Artificially placed gravel bar habitat in an abandoned channel of the Tombigbee River near Columbus, Miss.

Figure 8. Gravel bar habitats in flowing water systems.

Macroinvertebrates

13. Macroinvertebrates comprise four functional trophic groups: scrapers, shredders, collectors, and predators (Table 2, Figure 9). Scrapers are organisms such as snails, caddisflies, and other herbivores that feed on attached algae and associated bacteria and detritus. Shredders feed on wood, as well as decomposing and living plant material. Certain species of mayflies, caddisflies, blackflies, and all species of freshwater mussels are collectors which feed on fine particulate organic matter that has been recently deposited or is suspended in the water column. Predators, which either engulf or pierce their prey, range in size from small midges (less than 1 cm), to dragonflies, damselflies, dobsonflies, and fishes (Merritt and Cummins 1984).

14. The proportion of each functional group in a lotic system varies with stream order. In rivers greater than seventh order (Mississippi, Amazon, or Nile), the community usually consists of 90 percent collectors and 10 percent predators. Suspended particulate organic matter less than 1.0 mm such as bacteria and detritus is a large component of the available food source. Bivalves, including the unionids, as well as the Asian clam, *Corbicula fluminea*, can achieve their greatest abundance in these habitats.

15. Erosional zones of rapidly flowing waters, where all but the coarse substrate has washed away, have stone flies, mayflies, blackflies, and caddis flies adapted for attachment and clinging or avoiding current (Moon 1939). Invertebrates common in high-velocity water include true flies such as Blepharoceridae, Simuliidae, and Deuterophlebiidae and many species of stoneflies and mayflies. In headwater streams animals such as shredders and grazers obtain their food from the bottom or along shoreline areas (Cummins 1974, Cummins 1975, Vannote et al. 1980, and Minshall et al. 1983).

16. In some situations, trophic conditions (presence of suitable food) can be as important in explaining distribution of unionids as physical or chemical factors (Green 1971). Certain species of mussels are found only in small streams (Table 2). In these habitats bivalves are usually not common and are not restricted to large groups or beds as they are in systems greater than third or fourth order. Since mussels are nonmotile and dependent upon organic matter brought to them, they may be limited in upstream reaches where particulate organic matter is scarce.

Table 2

Major Functional Groups in Aquatic Systems

(from Merritt and Cummins 1984)

Group	Dominant Food	Representatives Small Rivers	Large Rivers
Scrapers	Periphyton	Coleoptera: *Psephenidae* Mollusca: Gastropoda	Ephemeroptera *Stenonema* spp. *Heptagenia* sp.
Shredders	Wood, decomposing and living plants.	Coleoptera: *Lara* sp. Diptera: *Tipula* sp.	Chironomidae *Glyptotendipes* spp.
Collectors	Decomposing and fine particulate organic matter	Trichoptera: *Cyrnellus fraternas* Pelecypoda: *Ptychobranchus* sp.	Trichoptera: Hydropsychidae Pelecypoda *Fusconaia ebena* *Amblema plicata* *Quadrula* sp. *Corbicula*
Predators	Living animal tissue	Odonata: *Calopteryx* sp. Megaloptera: *Corydalus* sp.	Diptera: *Chaoborus* spp. Odonata: *Gomphus* spp.

17. Maximum invertebrate diversity (aquatic insects, worms, and crustaceans) usually occurs in the midreaches of fourth- and fifth-order streams. These areas are characterized by large physical diversity, i.e., presence of pools, riffles, and runs, and an abundance of in-stream structure such as cobble, gravel, logs, brush and aquatic vegetation, and large annual temperature fluctuations (Vannote et al. 1980).

Fishes

18. For most species of fishes, the substrate characteristics are important mainly during breeding. Dissolved oxygen is not usually limiting in rivers, except for species such as brook trout (*Salvelinus fontinalis*), which survive only in cold water systems. The major problem riverine fishes encounter is maintaining themselves against a constant current. Some fishes
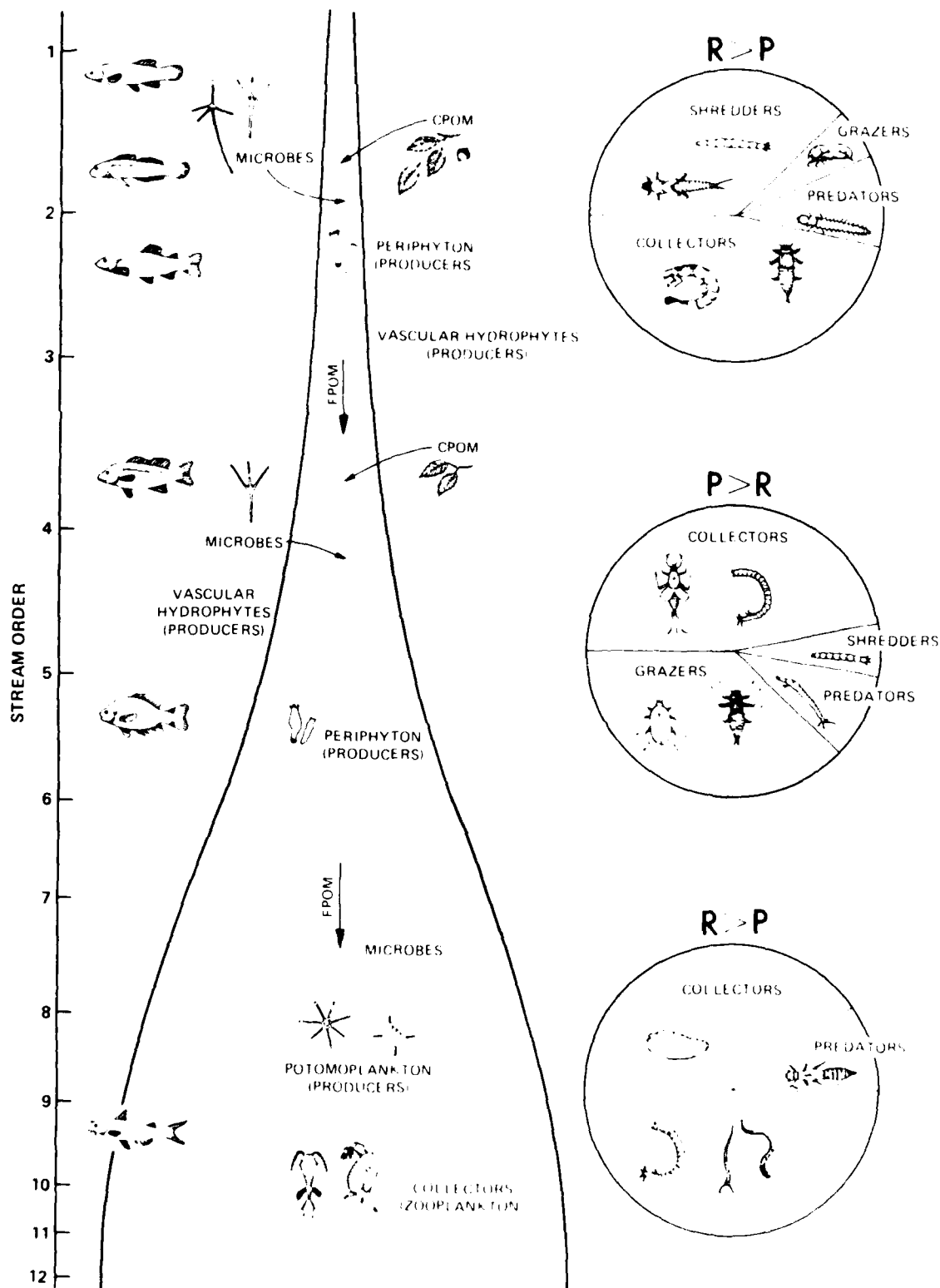
Figure 9. Functional feeding groups in flowing water systems. In many rivers after order 4, freshwater mussels are significant components of the invertebrate community (modified from Cummins 1974).

avoid this by seeking shelter; others inhabit low-velocity areas except while feeding.

19. Fishes common to headwater systems include darters, stone rollers, sculpins, and madtoms, which feed principally on invertebrates which they obtain from gravel or which are associated with brush and other forms of cover. Fishes common to large rivers include plankton feeders such as shad and paddlefish, and predators such as bass, sunfishes, and sauger. Bottom-feeding fish such as drum and catfish are common inhabitants in large rivers and feed on small mussels and *Corbicula*. Large rivers have a greater diversity and density of fishes, hence a greater opportunity for available fish hosts to carry immature stages of freshwater mussels. This is an additional reason for reduced density and diversity of molluscs in headwater streams. (See Part III for discussion of reproduction in bivalves and Appendix A for a list of fish hosts for mussels).

Anthropogenic Effects

20. In this country rivers are used as a source of water for domestic and industrial uses, as a repository for wastes, and as means of transporting bulk commodities. Channel maintenance, bank protection, clearing and snagging, and dredging are actions which have been commonplace since the latter part of the 19th century. In addition, the development of rivers such as the Ohio and Mississippi for navigation has led to construction of large, run-of-the-river reservoirs. These reservoirs cause reduced turbidity, longer water retention times, and higher primary productivity than existed prior to commercial navigation. They have been responsible for converting the fauna from those inhabiting shallow, fast-water habitats to those tolerant of lake-like conditions. Certain thick-shelled unionids (belonging to the genus *Dysnomia*) used to be more abundant when riffles and shoals were a significant aspect of large rivers (Stansbery 1971).

PART III: BIOLOGY OF FRESHWATER BIVALVES

Evolution

21. The bivalve clams and mussels of fresh waters are, in all aspects
of their anatomy, typical members of the phylum Mollusca and of the class
Bivalvia. While this is also true of most aspects of their somatic physiology
(including feeding mechanisms, digestion, growth, locomotion, and behavior),
they are clearly atypical in their life cycle patterns and nonmarine habitats.
The evolutionary background of these contrasting facts is important to an
understanding of the ecological constraints upon, and the general habitat dis-
tributions for, the few specialized genera of freshwater bivalves.

22. One of the most successful patterns of animal construction is the
molluscan plan, which is characterized by a soft, hydraulically moved body
contained within a hard calcareous shell. There are more than twice as many
species of molluscs as there are of vertebrates, and only the arthropods are
clearly a more numerous and more successful group (Russell-Hunter 1979, 1983).
There are probably 110,000 living molluscan species, and the biomass of cer-
tain of these species can dominate the lower trophic levels of many aquatic
ecosystems. In fact, in the global economy of the oceans, certain benthic
bivalves are second only to planktonic calanoid copepods in the annual calo-
rific turnover for animal tissues in food chains. Although molluscs are
largely marine, there are a few, highly successful nonmarine forms. Certain
bivalve genera are very important in the faunas of estuarine and fresh waters,
as are the more diverse groups of freshwater gastropods. The only terrestrial
molluscs are snails (class Gastropoda).

23. Freshwater bivalve molluscs belong to a limited number of largely
cosmopolitan genera classified in three lamellibranch superfamilies
(Unionacea, Corbiculacea, and Dreissenacea). Two of these are more important:
the Unionacea (the large freshwater mussels) and the Corbiculacea (the small
fingernail and pea clams). Throughout the world, the unionacean mussels are
generally associated with larger, relatively permanent river systems. In
their soft parts most freshwater mussels are structurally rather stereotyped.
Unionaceans show adaptive radiation principally in shell shape and shell
sculpture with their internal anatomy showing few of the adaptive specializa-
tions that give particular interest to functional morphology in most

20

superfamilies of marine bivalves. Specific anatomical modifications for particular habitats do not usually occur, although four tropical genera in the unionacean family Etheriidae (Yonge 1962) do show structural specialization for life in turbulent waters. River systems in the temperate latitudes of the world are populated by remarkably uniform genera of mussels. In the Northern Hemisphere most genera (including *Anodonta, Quadrula, Elliptio, Lampsilis,* and *Margaritifera*) are cosmopolitan in distribution; and for a few genera, closely similar sets of species are found not only in North America, but also in rivers of appropriate size in Northwest Europe, Central Asia, and Mongolia. Other species are clearly endemic, and even limited to particular river systems.

24. Though basically more uniform in structure, unionacean mussels differ from marine bivalves in having an obligatory parasitic stage in their life cycle, which can be species specific. After the fertilized eggs have been incubated in marsupial embayments of the exhalant gill cavity of the female mussel, they are released as glochidial larvae for a required period, as parasites on a vertebrate host (usually a fish species). After further growth (normally in a mutually formed cyst), juvenile mussels break out to settle on appropriate stable substrates. As in all animals with parasitic stages, reproduction in unionaceans is characterized by remarkably high numerical fecundity. It is important to reemphasize that, apart from this parasitic stage in their life-cycles, all other aspects of structure and function in freshwater unionacean mussels are typical of those found throughout the subclass Lamellibranchia and class Bivalvia.

Systematic Survey

Class bivalvia

25. Forming the most uniform of the three major classes in the phylum Mollusca, there are probably about 31,000 species of bivalves, all with the shell in the form of two calcareous valves united by an elastic hinge ligament. As in all molluscs, the shape of the shell is determined by the growth of the mantle (or pallium), the fleshy fold of tissues which enfolds the visceral mass and which, in the bivalves, has become elongate and laterally compressed so that all parts of the body (visceral mass, muscular foot, and all pallial organs including gills) lie within the mantle cavity and

the head is lost. (Bivalves were formerly referred to as the Mollusca-Acephala.) Obviously, normal cephalic sense organs would not be of much value within the mantle cavity and out of contact with the environment. In all molluscs the middle lobe of the mantle edge also bears sense organs, and in the bivalves these show their fullest development as chemoreceptors, as mechanoreceptors, and even as eyes. (Actually, no freshwater mussel has well-developed eyes like those of marine scallops, but all have light-sensitive patches of tissues in the posterio-ventral parts of the mantle edges.)

26. In the bivalves, as in all other molluscs, the mantle and its secreted shell form a single structural entity. The description found in most textbooks of two discrete valves united by a ligament of different origin is totally erroneous. Developmentally, a single mantle rudiment appears early in the larva, and although growth patterns are such that anterior and posterior embayments appear in the originally dome-shaped rudiment, there always remains a mantle isthmus. Usually, the material secreted by a mantle isthmus contains proportionately less crystalline calcium carbonate and proportionately more elastic tanned proteins, and forms the ligament of the bivalve shell. This elasticity is very important to the mechanical functioning of the bivalve.

27. In all bivalves the shell is closed by the action of adductor muscles, which run from one shell to the other. These, the largest muscles in any bivalve, have no single antagonist but can be stretched by several mechanisms, which include the elasticity of the horny hinge ligament and several kinds of hydraulic systems. The relative importance of each method varies in different types of bivalves. For example, in species of *Elliptio* and of *Margaritifera*, movement of blood into the sinuses of the foot and pedal protraction ventrally can force the shell valves apart and thus stretch the adductor muscles to their precontraction length. In contrast, in species of *Anodonta* and of *Strophitus*, the elasticity of the ligament is more important. In these, as in the Corbiculacea, Dreissenacea, and a wide variety of marine bivalves, the elastic ligament connecting the shell valves dorsally is under strain (tensile or compressive, depending on shell hinge structure) when the valves are closed. The force derived from this tends to open the valves. In fact when the adductor muscles of a bivalve contract, closing the shell, they are also doing the work which will subsequently reopen the shell valves. This work involves compression or extension of the "springs" of the ligament.

28. Although the Bivalvia are remarkably uniform in anatomy, there are three distinct subclasses, unequal in extent and in ecological significance. The great majority of living bivalves belong to the major subclass Lamellibranchia, which are characterized by having enormously enlarged gills used in filter feeding. All freshwater bivalves are lambellibranchs. The other two, more minor, groups comprise the subclasses Septibranchia and Protobranchia. The gills are replaced by a muscular septum in the septibranchs, a relatively rare group from moderate ocean depths. The sub-class Protobranchia is of greater evolutionary interest, since its genera are in many ways intermediate in form and function between the specialized filter-feeding lamellibranchs and more generalized molluscan stocks.

Subclass lamellibranchia

29. The diagnostic feature for lamellibranchs is their possession of a pair of enormously enlarged and folded gills. Each lamellar gill has many elongated filaments, and although it is homologous both functionally and morphologically with the ctenidium in gastropods (and all other molluscs) in terms of its blood vessels and arrangement of cilia and so on, is far more extensive then is required for the respiratory needs of the animal. It is now the major organ of food collection in these filter feeders. Briefly, a water current through the mantle cavity is created by the lateral cilia. This flows through between the filaments of the ctenidium from the inhalant part of the mantle cavity to the exhalant region. Any particulate matter remains on the inhalant face of the gill, and frontal cilia and mucus are used to make chains or boluses of material to pass to the mouth. The structures and functions involved in this diagnostic feeding mechanism are described more fully in the following paragraph.

30. In many time-honored and popular classifications of the bivalves, the many superfamilies of lamellibranchs were divided between two orders Filibranchia and Eulamellibranchia. The ordinal name Filibranchia was used for those bivalves with ctenidial filaments in their lamellar gills held together by ciliated junctions. In contrast, the superfamilies of the order Eulamellibranchia were defined as having gill filaments united by fused tis-sues, thus forming a mechanically stronger and more efficient filtering apparatus for feeding. Although attractive on functional grounds, this divi-sion is unacceptable phyletically since the eulamellibranch condition has been independently evolved in several different stocks of bivalve families. Better
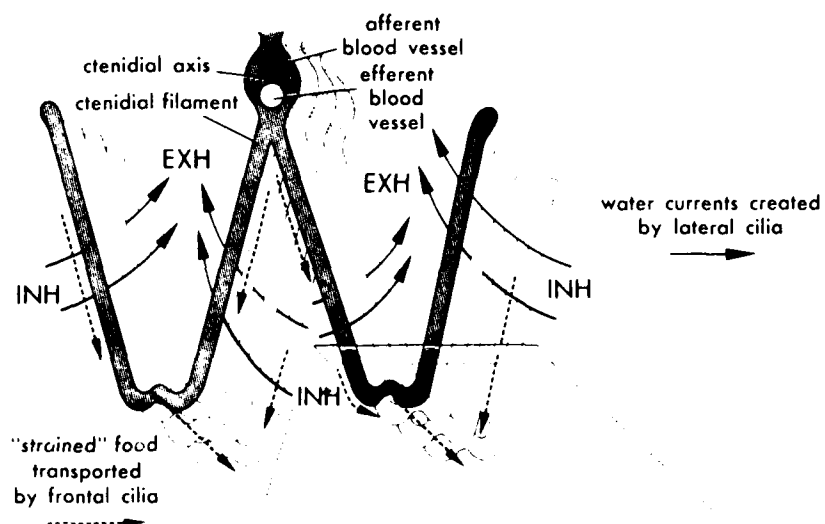
modern classifications do not employ these two ordinal names. Among fresh-
water forms, the Dreissenacea show the filibranchiate condition, but all the
Unionacea are eulamellibranchiate.

Superfamily Unionacea

31. There are several alternative ordinal arrangements for the many
well-established superfamilies of lamellibranch bivalves. Many neontologists
employ a relatively conservative classification which divides the subclass
Lamellibranchia into six orders containing living forms, and assigns the
superfamily Unionacea to the order Schizodonta. The superfamily or suborder
Unionacea (or Unionoidea) comprises freshwater bivalves, dimyarian and rela-
tively symmetrical, mostly with schizodont hinges, with mantle edges almost
completely unfused, with a large plough-shaped foot, and with the two large
ctenidia in four relatively posterior demibranchs which can be used as
marsupia in brooding larvae. Recent authorities (including Burch 1973) place
the unionaceans of North America in three families, separating both the
Margaritiferidae and the Amblemidae from the large worldwide family Unionidae,
but there remains some resistance to these separations. Elsewhere within the
superfamily, the family Mutelidae is largely limited to the Southern Hemi-
sphere, and the family Etheriidae includes the peculiar oysterlike forms from
turbulent rivers in the tropics. The cosmopolitan family Unionidae comprises
a very large number of species and subgenera, although it should be noted
that, in many classifications of freshwater mussels, "splitting" at the
generic and subfamilial levels is probably excessive. Compared with the
characters used in the generic systematics of most families of marine
bivalves, those used in the Unionidae are relatively trivial.

Filter-Feeding Mechanism

32. The majority of bivalves (perhaps 29,000 out of 31,000 living
species including all Unioniacea) have essentially the same feeding process.
The following description would apply to any of them, although Figure 10 is
largely based on the structures in mussels such as *Mytilus*. In all
lamellibranchs, the lateral cilia produce the water current between adjacent
filaments. This water passes ventrally into the inhalant part of the mantle
cavity, and thence through the gills to the exhalant chamber above and within
them. All food organisms and all suspended material are accumulated on the

a. Stereogram of folded filaments in ctenidium

afferent blood vessel

ctenidial axis

ctenidial filament

efferent blood vessel

EXH

EXH

water currents created by lateral cilia

INH

INH

INH

"strained" food transported by frontal cilia

exhalent cavity = "suprabranchial"
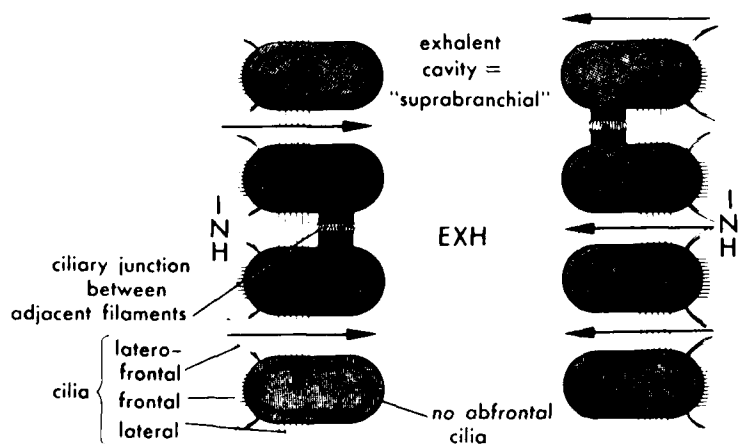
b. Horizontal section through a demibranch (a half ctenidium)

ciliary junction between adjacent filaments

INH

INH

EXH

cilia

latero-frontal

frontal

lateral

no abfrontal cilia

Figure 10. Archetypical gill structure in lamellibranchs (from Russell-Hunter 1979)

inhalant faces of the gill lamellae. Such material and food are then moved by the frontal cilia toward the ventral edges of the gills and accumulated in the food grooves with some mucus. As can be seen in Figure 10, the food grooves result from an infolding of the frontal surface of the gill filaments. In them the frontal cilia are functionally modified and beat anteriorly, so that the food material passes anteriorly along the ventral edges of the gills to between the labial palps. Here again, sorting is carried out on a size basis (Figure 11).

33. Fine material is carried by cilia into the mouth and into the esophagus and stomach, where it undergoes further sorting. Coarser particles accumulate at the edges of the palps and are periodically thrown off by muscular twitches onto the mantle wall. This material, which has been filtered off by the feeding structures but has never entered the gut, is usually called pseudofeces; it is collected by the cleansing cilia of the inside of the mantle wall into ciliary vortices whose arrangement varies in different bivalves. In almost all species the pseudofeces are finally expelled from the bivalve by spasmodic contractions of the adductor muscles which force water, together with the accumulated pseudofeces, out through the normally inhalant openings to the mantle-cavity. All bivalves including unionids show these "spontaneous" spasmodic contractions of the adductor muscles, which thus have a cleansing function. It should be mentioned at this point that the anus and the renal and genital openings are in the exhalant part of the mantle cavity in bivalves, as in all molluscs, and thus expulsion of the wastes or reproductive products is not accomplished by these spasmodic cleansing movements, but by the normal and continuous water flow of the feeding current.

34. Two points should be noted in the diagram of the horizontal section through a half-gill (Figure 11). An additional group of cilia, the laterofrontals, have arisen and serve as a part of the filtering mechanism. In a classic series of research reports, Daphne Atkins (1936; 1937a, b; 1938, 1943) reported beautiful studies by light microscopy on the variation of laterofrontal cilia and on the ciliary mechanisms of various lamellibranch groups. More recently, use of the scanning electron microscope has shown the laterofrontals to be compound cilia, with a finely pinnate structure which greatly increases their efficiency in the trapping of food particles and flicking them onto the frontal collecting tracts (Figure 12). On the other hand, the exhalant sides of the filaments do not have rows of abfrontal cilia
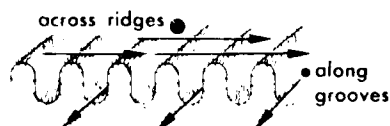
a. On a simple sorting surface, large particles are carried across the ridges, fine particles along the grooves
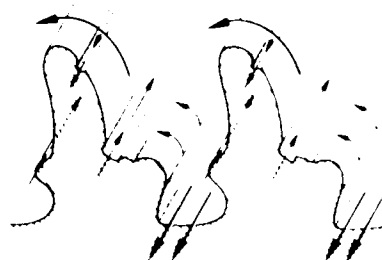
b. On more complex sorting surfaces, five categories of particles can be sorted in different directions

Figure 11. Ciliated sorting surfaces, which are used externally and internally in molluscs for the mechanical separation of particles of different sizes (from Russell-Hunter 1979)

such as are found on the ctenidia of all other kinds of molluscs. Functionally, this implies that there is no material which penetrates to the exhalant part of the mantle cavity and has to be cleansed off the gill surfaces.

35. A further point is that in such forms as *Mytilus* and *Crenella*, the adjacent filaments are held together only by occasional ciliary junctions, which function rather like modern dress fastenings of Velcro. In certain other bivalves, such as the unionids, these ciliary junctions are replaced in adults by tissue fusion between adjacent filaments. This character of the nature of the interfilamentary junctions was formerly used in the classification of the bivalves. Recently, however, it has been realized that tissue fusion has been evolved independently in several lines of clams.

36. Incidentally, there is evidence of a totally different sort that the significance of the vast size of the lamellibranch gill is alimentary and not respiratory. If measurements are made of the oxygen consumption of clams, it can be calculated that at the oxygen tensions of their environment, gills of approximately one-fiftieth of the surface area of those developed would suffice for the entire respiratory exchange of such clams.

37. From time to time, claims have been made that mucous sheets are important in the filtration by the gills of lamellibranchs. These have all proved to be wrong, based either on misinterpretation of data on clearance

27
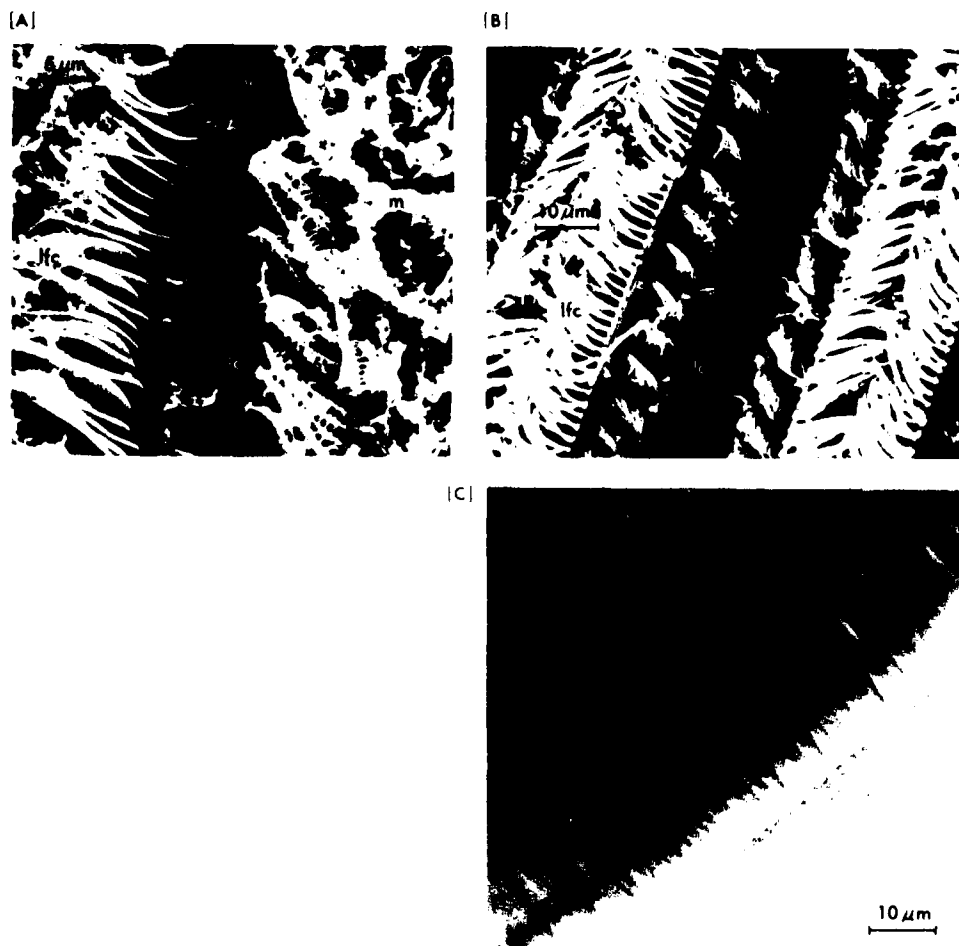
Figure 12. Bivalve laterofrontal cilia as cirri. The great effi-
ciency of the lamellibranch gill as a filter-feeding mechanism
depends upon the "additional" group of cilia (the laterofrontals) on
each ctenidial filament (see Figure 10 for orientation). A and B:
Scanning electron micrographs of adjacent pairs of ctenidial
filaments in fact view. C: Interference photomicrograph of the
edge of a living gill filament (all from the mussel _Mytilus_). In
all photographs the finely pinnate nature of these laterofrontals as
compound cilia (or cirri) can be seen. On the right-hand filament
in A, the partially extended laterofrontals have been fixed as they
cleansed from a small mass of mucus; while both filaments in B
(a preparation which had been stimulated with serotonin or
5-hydroxytryptamine, at a concentration which is known to increase
water flow through the gill while decreasing particle retention)
have the laterofrontals (lfc) folded inward over the frontal cilia,
thus "opening" the spaces between the filaments and increasing the
efficiency of water propulsion by the lateral cilia (lc), which are
seen to be organized in metachronal waves. In the living condition
(C) the laterofrontals are shown extended and beating in metachronal
rhythm, and thus this photomicrograph constitutes a "food-
particle's-eye" view of the filtering apparatus of a typical
lamellibranch bivalve. (From Russell-Hunter 1979, photos courtesy
    of Dr. C. Barker Jorgensen of the University of Copenhagen).

rates or on direct observations on injured or unhealthy clams. The latter misunderstanding arises from the fact that many lamellibranchs will respond to the traumatic removal of one shell valve and attached mantle by "shutting down" the gill by contraction of muscles in the ctenidial filaments, withdrawal of blood from the gill as a whole, and a massive secretion of mucus over its surface for protection. If the bivalve recovers, all of this mucous sheet is rolled up and moved through the rejection tracts to finish as pseudofeces on the remaining mantle wall. In a fully extended and healthy gill, there is only a little mucus on the frontal collecting tracts, and water passes freely between the laterofrontal cilia into the exhalant chambers. Filtration of particulate material that will be "accepted" and passed over the labial palps into the mouth is carried out entirely by the spaced combs of the compound laterofrontals, which throw food particles onto the frontal collecting tracts without any mucus entanglement.

38. This feeding method is in complete contrast not only to those of gastropod filter feeders like *Crepidula*, which spin a mucous net as one of their feeding mechanisms, but also to those of such forms as Urechis (minor phylum Echiuroidea) and to all sea squirts. Those filter feeders, using a mucous net or mucous sheets, are apparently able to retain large colloids, but there is no good evidence of such forms being involved in adsorption of organic molecules out of solution. In recent years there has been a revival of interest in older theories (Putter's hypothesis) of direct uptake of dissolved organic materials from seawater by soft-bodied invertebrates like worms and molluscs. Many aquatic animals can be shown to leach organic molecules outwards into the medium. Double radioactive labelling has now established that net uptake (trophic "gains" to the individual animal) can occur in a few marine forms but in no freshwater ones. It is worth reemphasizing here that although bivalves such as marine mussels can be shown to take up dissolved organic molecules such as glucose and amino acids, detailed work on the net effects of the transport systems involved, along with assessments of the amount of dissolved organic matter available in unpolluted seawaters, demonstrates that the amounts that can be taken up could not constitute as much as 1 percent of the total energy requirements of these animals. Although some marine invertebrates, including certain polychaetes and pogonophorans can cover a major part of their maintenance requirements by uptake of dissolved

amino acids from sediments rich in organic material, this is clearly not the
case in bivalves, despite their remarkably high surface to mass ratios.

39. In summary, larger lamellibranch bivalves are true ciliary filter-
feeders, relying only on the spacing of their laterofrontals (adaptively
adjusted to each specific habitat and capable of temporary shifts in "mesh
size" by variation in the hydraulic turgor of their filaments), and do not
need recourse to sheets of mucus, or to direct active transport of dissolved
organic molecules for their nutrition.

40. In most bivalves, considerable shifts are possible both in rate of
water transport and in gill porosity (or filter size), and it is presumed that
these can occur in response to environmental changes such as shifts in the
nature and concentration of suspended material. The functioning of the
ctenidial filter is known to be under both neurosecretory and direct neural
control (see Jorgensen 1975) involving capacity to vary not only the rate of
beat in the lateral (water-propelling) cilia, but also the angle of beat in
the laterofrontals, and the level of hemohydraulic turgor of the filaments.
Most research on adjustments in filter-feeding rates has been carried out on
marine bivalves such as _Mytilus_, or on tiny corbiculacean clams by Burky and
his associates (Burky 1983), and no parallel research has yet been done on
unionacean mussels. Despite this, some general features of the response
adjustments can be noted. In some cases, clearance rates and water transport
rates can vary independently. In many cases (including some corbiculaceans)
there is an inverse relationship between clearance rates and the concentration
of suspended material. In contrast, there is evidence that some bivalves
maintain their water transport rate at a constant level independent of par-
ticle concentration. Specific responses are complex and may reflect adjust-
ments to local circumstances (microhabitat) or to seasonal ecology. Finally,
any attempts to quantify nutritional intake in lamellibranchs must assess the
rates and organic content of pseudofeces production. These must be deducted
from any intake values established from filtration clearance rates to
establish calorific (or organic carbon) values for true ingestion.

Gut Function and Digestion

41. In all molluscs the alimentary canal is extensively ciliated, with
many internal surfaces adapted as sorting areas, similar to the external

surfaces of the bivalve labial palps (see Figure 11). Functionally, digestion is mixed: both extracellular and intracellular breakdown is carried out (in all molluscs except higher Cephalopods). The typical molluscan gut (as found in all lamellibranchs, and in the majority of more primitive gastropods) is organized to deal slowly but continuously with a steady stream of finely divided (usually plant or bacterial) material passing in from the feeding organs. The gut requirements to deal with continuous microherbivory, or ingestion of individual tiny plant cells, are essentially the same in primitive snails which ceaselessly graze by radular action and in filter-feeding bivalves.

42. The organization of this primitive gut pattern is dictated by the need to deal with quantities of finely particulate food, embedded in a mucous strand with some inorganic material, which passes more or less continuously into the gut. Thus the physiology of primitive molluscan guts contrasts markedly with the intermittent feeding followed by cyclical processes of digestion so characteristic of vertebrates and the more highly organized invertebrates, including the more specialized carnivorous molluscs. Mechanisms for handling a continuous but slow stream of finely divided food material have been evolved in other filter-feeding animals, but nowhere have ciliated surfaces become so highly organized for continuous processing of material as within the molluscan alimentary canal. Most of the gut is ciliated, and the stomach and its associated diverticula have especially complex ciliary sorting tracts. Another characteristic feature of these primitive molluscan guts is the possession of a peculiar secreted structure: the crystalline style. In a few more primitive gastropods and in the protobranchiate bivalves, the style is secreted in, and occupies most of, the lumen of the first part of the intestine immediately after the stomach cavity. In the great majority of bivalves and filter-feeding snails the style sac is completely separate from this anterior intestine (Figure 13). In a few bivalves there are anatomical connections between the style sac and the typhlosole side of the anterior intestine, but the lumen of the sac is always functionally separated from the lumen of the intestine, except in some primitive snails. In the typical gut (Figure 13), the mouth opens into a short ciliated esophagus, the cilia of which may be arranged in spiral rows which can impart a twist to the rope of mucus with contained food particles coming in from the feeding organs. This opens into a subglobular stomach from

31
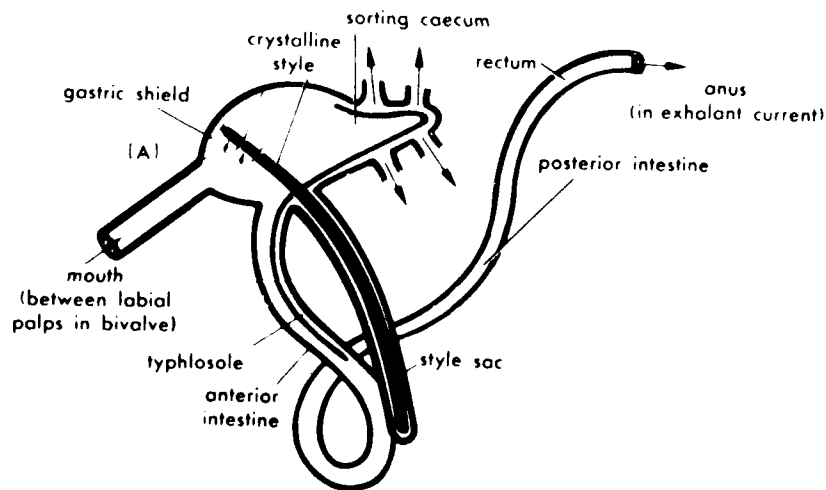
a. The arrangement of the alimentary canal in a filter-feeding
mollusc. This gut is organized for the slow but continuous
processing of a stream of finely divided food material.
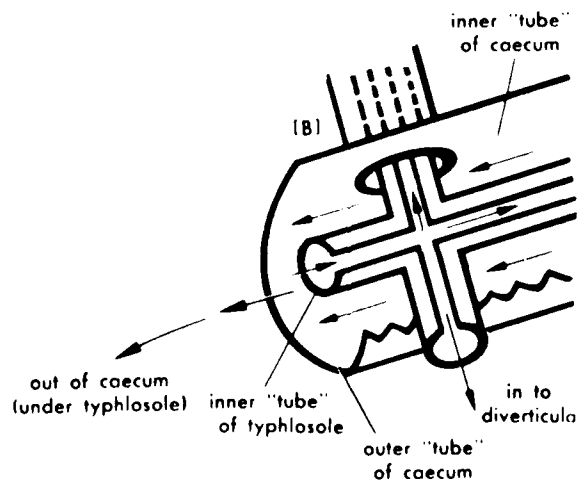
b. Part of the cecum in a lamellibranch bivalve.
The typhlosole forms a tube within each tubular
root of digestive diverticula, allowing further
sorting.

Figure 13. Typical gut arrangement of a filter-feeding mollusc
(from Russell-Hunter 1979, modified from Morton 1958 and
Owen 1955)

which open, ventrally, the openings of the anterior intestine and of the style sac and, posteriorly, the paired basal ducts of the digestive diverticula. The anterior intestine has a fold, which is often elaborate, in its wall. This typhlosole usually extends along the floor of the stomach and around the openings of the digestive diverticula, sometimes in a complicated fashion (Figure 13). After the typhlosole ends in the anterior intestine, the rest of the gut tube (posterior intestine and rectum) is anatomically undifferentiated. It ends in the anus, which, as was already stressed, discharges in the exhalant part of the mantle cavity in all forms.

23. The hyaline rod of hardened mucoprotein which is the style protrudes from the style sac into the stomach, and its free end bears on a cuticularized patch called the gastric shield. The style is formed in the lower part of the style sac (although it may be secreted by cells of the typhlosole in some cases). It is continuously revolved by cilia lining the intermediate parts of the style sac, and, in all lamellibranchs at least, the direction of revolution is clockwise if viewed from above the gastric shield. The hyaline material is impregnated with several secreted enzymes which always include amylases and glycogen-breaking enzymes (in a few cases lipases and cellulose-breaking enzymes have been detected). The style thus acts as an enzyme store allowing a slow but continuous release as the mucoprotein softens in the higher pH of the stomach and the style is ground off against the gastric shield. It also acts as a stirring rod for the contents of the stomach lumen and in many molluscs can be seen to act as windlass onto which the mucous rope of food material is being continuously wound or, in fact, pulled in from the esophagus.

24. The rates of style revolution and of style wear are low: one revolution takes from 3 to 12 sec, and about 4 mm of style per hour is worn off in an actively feeding, moderately large bivalve. In some deposit-feeding bivalves, there is also trituration of food material by the relatively massive style acting against the gastric shield as a sort of millstone. In a few bivalves where there are connections between the anterior intestine and the style sac, some particulate material may be recycled from the intestine by passage into the style sac and incorporation in the style material and thus transported back to the stomach. Style-bearing molluscs all exhibit breakdown and resorption of the style under unfavorable conditions.

45. The pH patterns of the molluscan gut are characteristic: in a typical bivalve they can range from pH 4.4 in the style itself through about 5.7 in the stomach cavity and up to pH 7.0 in the rectum. The higher pH of the stomach fluid helps bring about the disintegration of the style, although the style itself helps control the pH of the stomach contents and is believed also to exert some buffering action. The neutral pH of the posterior intestine and rectum is associated with a region of water reabsorption which serves to consolidate the feces produced. It is obviously necessary to con- solidate fecal material to avoid self-fouling of the feeding mechanism. Some bivalves are so successful in this that their fecal pellets or strands persist for long periods of time in marine bottom deposits, and in some cases the feces of tellinacean clams can be identified to species by patterns impressed on them by the typhlosole and ciliary tracts in the more anterior parts of the gut, before consolidation.

46. The other important function of the stomach, sorting of particulate material, is carried out largely in the posterior cecum, from which arise the major ducts of the digestive diverticula. The actual details of the ciliary sorting areas differ considerably in different molluscs, but they are all basically made up of surfaces covered with grooves and ridges functioning in essentially the same fashion as the labial palps in bivalves (see Figure 11). In general, their functioning directs larger and heavier particles toward the anterior part of the stomach cavity (and if not broken down on recirculation, thence to the anterior intestine and rejection), while finer particles are carried across the ridges and grooves and recirculated again and again past the openings of the ducts to the digestive diverticula. Thus, after the extracellular digestion of the stomach lumen, dissolved material and finely particulate food pass into the tubules of the digestive diverticula. In the walls of these tubules are phagocytic cells. In most bivalves and the more primitive gastropods, these take up the particulate material, and a further intracellular digestion takes place. Even the fine material which is not digested is phagocytized and formed into spherules which pass back in a rejec- tion tract and thence under the typhlosole to the intestine. No material can pass into the hindgut of such a mollusc until it has circulated at least once across the sorting surfaces and more usually traveled around the stomach more than twice.

47. In general, in all molluscs (with the possible exception of a few
advanced cephalopods), the initial processes of extracellular digestion have
to be followed by phagocytosis and thereafter by intracellular digestion. The
cells lining the finer tubules of the digestive diverticula are the site of
this cellular ingestion and subsequent digestion, and it appears that in many
molluscs the bulk of proteolytic enzymes come into play only within the "food
vacuoles" of the cells of the diverticula. It should be noted that the appli-
cation of the term liver to this mass of tubules which forms the digestive
diverticula in molluscs is totally erroneous, although common in textbooks.
The many functions of the diverticular cells include absorption, phagocytosis,
secretion, and possibly some excretion. In the bulk of the microphagous forms
including unionace mussels, the absorptive and phagocytic functions are the
only important ones.

Locomotion and Behavior

48. With the exception of the pericardium and certain renogenital
ducts, the coelomic body cavity in molluscs is replaced early in development
by extensive systems of hemocoelic spaces filled with blood. The low-pressure
circulation of relatively large volumes of blood would be inadequate for the
respiratory needs of any more active (less "sluggish") animals. The blood in
the hemal meshwork of all molluscs has another functional importance, since it
is used as a hydraulic skeleton to transmit forces generated by _distant_ muscle
contraction. A few minutes spent carefully watching the movements of any
living snail or mussel should convince an observer on this point. The charac-
teristically extensible soft parts of molluscs such as tentacles, the foot,
the siphons, and so on, can all be rapidly withdrawn by muscular contraction,
but are only slowly extended again by blood pressure, by blood being shifted
into them from another part of the molluscan body. Strictly speaking, it is
correct to refer to this as a _hydraulic_ skeleton since forces are transmitted
by _movements_ of fluid. In molluscs, the underlying anatomical pattern of
obvious retractor muscles within each structure, without obvious antagonists
locally placed, is characteristic. This reliance on distant antagonists and
the unchanging total blood volume in the hemocoelic hydraulic skeleton
together are responsible for many of the peculiar features in the mechanics of

molluscan locomotion and other movements. For example, limitations arise in the number of extensile structures which can be dilated and protruded at one time.

49. Adult unionid clams do not move much, but juvenile clams (<2 cm) are much more active. Both sizes have similar muscular structures (approximately isometric) and similar mechanical capacity for locomotion. Typical unionids, like many unspecialized marine bivalves, are set up as shallow burrowers with a relatively large muscular foot and little development of the posterior mantle edges into siphons. They have a symmetrical and usually moderately globose shell, with the dimyarian condition of more or less equal anterior and posterior adductor muscles, and with two pairs of pedal retractor muscles attached to the shell near the adductors.

50. Mechanically, burrowing involves the shell valves and the foot which provides alternate fixed anchorages against which movement can take place (Figure 14). A burrowing cycle can be considered as starting with the shell valves gaping and being pushed against the substrate by the ligament's elasticity along with water pressure in the mantle cavity and blood pressure in the mantle edges. In this condition of shell or penetration anchorage, the adductor muscles are relaxed and stretched. With the shell valves fixed, contraction of the circular and transverse muscles within the foot causes it to probe downward, the siphons becoming closed as the foot is extended to maximum length. At the end of this stage, the tip of the foot begins to dilate, and partial dilation is immediately followed by a relatively sudden contraction of the adductor muscles (with the siphons closed). This contraction frees the shell valves from their anchorage in the substrate and at the same time forces some water out of the mantle cavity around the foot. This drives much more blood into the foot, thus completing its terminal dilation and forming a new pedal anchorage. Contraction of the pedal retractor muscles then pulls the whole body of the clam down toward the foot, the shell valves remaining closed by the adductors until the bivalve is poised for the beginning of another burrowing cycle.

51. In the more globose unionids, there can be a further refinement of the process of pulling down on the pedal anchorage. Contraction of the anterior pedal muscles can occur a little in advance of the other movements and will cause the clam to be pulled forward obliquely on the pedal anchor (with the dorsal or ligament side of the shell being pulled into the substrate

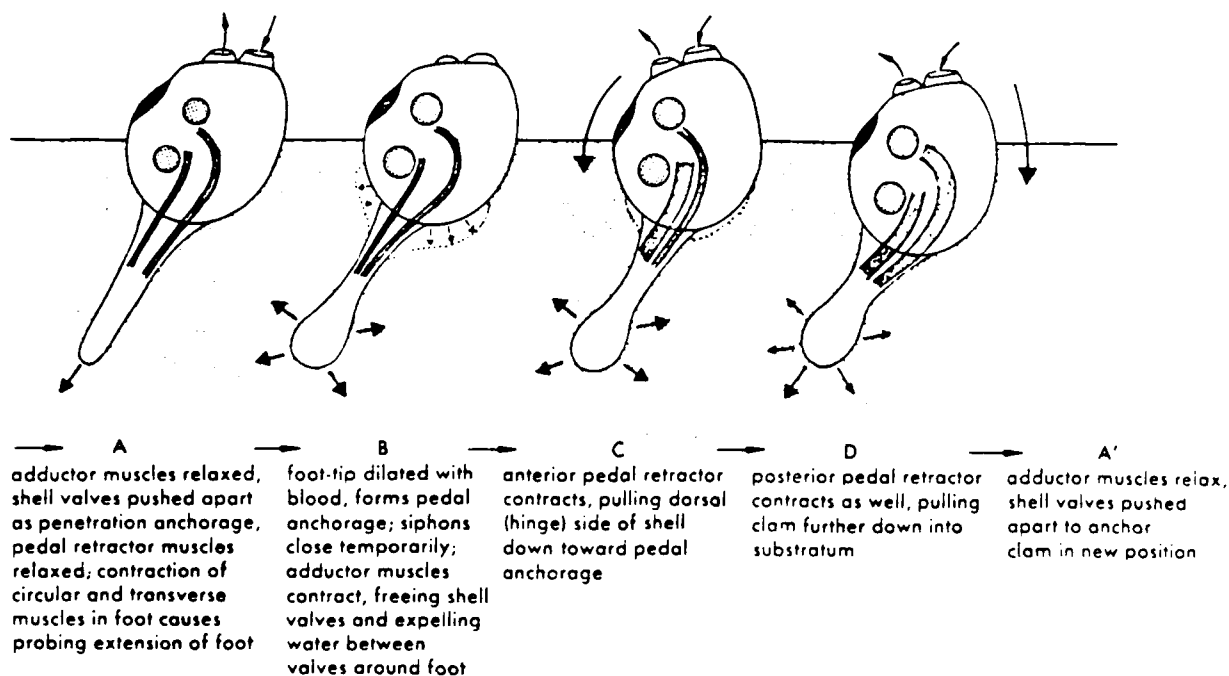| A	B	C	D	A'
adductor muscles relaxed, shell valves pushed apart as penetration anchorage, pedal retractor muscles relaxed; contraction of circular and transverse muscles in foot causes probing extension of foot	foot-tip dilated with blood, forms pedal anchorage; siphons close temporarily; adductor muscles contract, freeing shell valves and expelling water between valves around foot	anterior pedal retractor contracts, pulling dorsal (hinge) side of shell down toward pedal anchorage	posterior pedal retractor contracts as well, pulling clam further down into substratum	adductor muscles relax, shell valves pushed apart to anchor clam in new position

Figure 14. The stages of burrowing locomotion in a stylized bivalve. The cycle can be repeated many times, with alternate points d'appui being provided by the opening gage of the shell valves (the shell or penetration anchor) and by the dilated tip of the foot (the pedal or retraction anchor) (from Russell-Hunter 1979, modified from Trueman 1966 and 1968)

somewhat faster). At this point the siphons will reopen, and contraction of the posterior retractors will cause the shell to rotate in the opposite direction (the valve gape being now preferentially pulled down). The rotation will work the clam further into the substrate before the adductor muscles relax and the valves are separated by the elastic action of the ligament and by fluid pressure to form a new shell or penetration anchorage for yet another cycle. Size becomes important in burrowing if mussels have become totally exposed and are lying on one valve on the surface of the substratum. In such circumstances, smaller adult and juvenile unionids can readily reburrow, the first downward probe of the foot being to one side of the mussel, and the first contraction by the pedal retractor muscles down onto the pedal anchorage will

bring the mussel erect with its midline in a vertical plane. After that, a
series of activity cycles will take the mussel down into the substrate. Under
some circumstance, these first stages of reburrowing may not be possible for
the largest unionids and for those (e.g., *Quadrula*) with the heaviest shells.

52. Large unionids are essentially fixed sessile organisms. Apart from
monitoring the water flow through their mantle cavity (for which they use
pallial internal sense organs such as the osphradia), their only contact with
the environment is by way of the mantle edge tentacle ringing the inhalant and
exhalant openings of the mantle cavity. Looking down through water on healthy
unionids in a natural mussel bed, one may see posterior shell edges in a few
cases; but most individual mussels will show only as a figure eight of pig-
mented pallial tentacles close to the surface of the substratum. There is
abundant circumstantial evidence that these tentacles include light-sensitive
sensillae as well as mechanoreceptors and probably chemoreceptors. Appropri-
ate stimuli to any of these can provoke tentacle and mantle edge retraction
and closure of the shell valves posteriorly. Thus anglers and commercial
mussel fishermen can catch freshwater mussels.

53. Smaller unionids can move horizontally, half-buried in the sub-
stratum, but using the same alternate anchorage pattern in their locomotion.
It has been suggested that some young unionid mussels live and grow in limited
areas of stable sand before migrating to more variable and gravelly substrates
to spend their adult lives. For other species, some populations are known
where juveniles clearly coexist with adults. As will be discussed, there is a
lack of information on the movements and behavior of newly settled
postglochidial stages of unionacean mussels.

Reproduction and Early Development

54. The great majority of marine lamellibranchs are dioecious (or non-
simultaneous protandric hermaphrodites) and produce large numbers of rela-
tively small eggs which give rise to free-swimming planktonic larvae. These
ciliated veliger larvae usually pass through prodissoconch and dissoconch
(characteristically bivalved) stages, all of which are free-swimming in the
water column, before settling out of the plankton into the appropriate adult
benthic habitat. The only freshwater bivalve which has a planktonic veliger
stage is *Dreissena polymorpha* (Dreissenacea). The corbiculacean clams are

hermaphroditic with few relatively large eggs, held marsupially through
development until release as miniature adults. The unionacean mussels include
both dioecious and hermaphroditic species, but all produce very large numbers
of relatively small eggs again held marsupially but released as small
specialized parasitic larvae or glochidia. This has long been cited as an
adaptation for life in riverine habitats, for which free-swimming veliger
larvae would be inappropriate.

55. Most larger unionids spawn the glochidial young in enormous numbers
(up to 10^5 or 10^6) through the exhalant aperture along with the outgoing water
from feeding, although species of *Lampsilis* show more specific responses in
their glochidial release (Kraemer 1970). The newly spawned glochidia are
never free-swimming, and all show obligatory parasitism of aquatic vertebrates
as a necessary stage in their life cycle (Arey 1932a,b,c; Baer 1952; Fuller
1974). The glochidia of many species are armed with hooks and hinged spines,
while most can secrete temporary byssus threads from the foot or spin a mesh
of mucous threads from the posterio-ventral part of the mantle cavity. All of
these apparently help achieve surface contact with, and infection of, the host
(in some cases through its feeding, and in many cases by its gill ventilation
currents). In the usual fish hosts, contact is followed by attachment, using
spines or byssus to the host's gills or fins. A tissue reaction takes place,
and each larval parasite becomes enclosed by growth of the host epidermis;
then the embryonic mantle secretes enzymes and digests and assimilates part of
the host tissue (Arey 1932a). Subsequently, the glochidium undergoes a meta-
morphosis involving complete histolysis of the larval organs. Once the adult
organs are formed, the young mussel breaks out of the host "cyst" and falls to
the bottom to grow to adult size. For several species, there is clear evi-
dence that specific hosts, either fish or urodeles, are required for success-
ful metamorphosis (Fuller 1974, and references therein). Newly spawned
glochidia will attach to a wide variety of hosts, but are sloughed off by most
before metamorphosis. Further, even the normal species of vertebrate host can
acquire an immunity to subsequent glochidial infection (Arey 1932c; Baer
1952). Some even more specialized parasitic development has evolved, as in
the case of an African mutelid mussel where each glochidium has a temporary
filamentous tentacle more than 70 times its mantle length, and the host
cyprinid fish is invaded by a postlarval parasite which is more like a fungal
hypha than a cyst (Fryer 1961).

56. Clearly host specificity can create a particularly fragile link in the continuity of any mussel life cycle. Even given the cases of those mussels where several species of fish can be efficient hosts, it is obvious why high numerical fecundity and an iteroparous, long life-span are character-istic features of the Unionacea. It has been pointed out (Fuller 1974) that those North American unionid species that can successfully parasitize a wider variety of host fish species include several of the more ubiquitous and suc-cessful mussels such as *Anodonta grandis* and *Amblema plicata*.

57. After release of the metamorphosed postglochidia from the host, successful recruitment to an adult population involves yet another fragile link as the juvenile mussels must locate a suitable substrate for further growth. In some species, specific contour stability and deposit texture may be more necessary for juveniles than for large adults. Surprisingly little is known about the growth and ecology of newly metamorphosed and juvenile unionids. Work on population dynamics in the river Thames (England) by Negus (1966) has provided some growth data on juveniles of *Anodonta anatina* and two species of *Unio*, but even for the more abundant North American mussel species, detailed quantitative data on juveniles are lacking. Recruitment to adult populations in unionacean bivalves (including those of gravelly shoals in major rivers) may well prove to have irregularly cyclic patterns of success, similar to those known to occur in longer lived barnacles of the upper marine littoral and in natural coniferous forests.

Commercial Uses

58.   A pearl forms in a bivalve mollusc when nacre is secreted over a piece of foreign material lodged between the shell and the mantle.   Thick-shelled, long-lived unionids are the best sources of large, well-shaped natural pearls.   The first references to natural freshwater pearls in America were in the accounts of Hernando De Soto in the early 1500s (Sweaney and Latendresse 1982).   The American Indians in Virginia, Tennessee, and the Ohio Valley made extensive use of pearls for ornaments and trade.   Evidently they encountered pearls when they opened mussels for food.   There is a large market for natural freshwater pearls in this country.   Buyers such as the Tennessee Shell Company and American Shell Company purchase freshwater pearls for jewelry.   It is not uncommon to collect pearls worth $100 or more, and the commercial dealers regularly display gem-quality natural pearls valued at thousands of dollars.   Sales of pearls in this country have increased from $54 million in 1977 to more than $600 million in 1984 (Sitwell 1985).

59.   A frequently asked question concerns the edibility of freshwater molluscs.   There are many reports that freshwater mussels were eaten in this country during the Great Depression and are still consumed by certain groups of people.   The University of Tennessee conducted taste tests on mussels and concluded that *Megalonaias nervosa (gigantea)* is edible when properly prepared (Peach 1982).   American Indian tribes consumed the meat of large quantities of mussels (Matteson 1955, Ortman 1909).   Freshwater mussels are eaten by raccoons, muskrats, and otters (Imlay 1971, Van der Schalie and Van der Schalie 1950).

60.   In the 1800s and early 1900s the primary use for mussels was for processing their shells into buttons.   Circular pieces were cut from smooth, thick shells of some species (family Lampsilidae) and processed into pearl buttons for shirts and other garments.   This use of shells stopped in the 1950s with development of the plastics industry.

61.   A few years later it was found that inserts made from shells collected in the United States could be used to make cultured pearls.   The thick, white shells of species such as *A. plicata* or *Quadrula quadrula* are now shipped to the Orient, where they are cut into cubes, ground into spheres, and

inserted into oysters. In 1966-67 the Japanese imported over 25,000 tons of shell from the United States; however, this volume has now declined to about 4,000 to 6,000 tons per year (Peach 1982).

62. The demand for shells from this country provided impetus for developing an industry for collecting and processing shells similar to that which exists for collecting and processing furs from wild animals. Traditionally molluscs were collected alive from rivers with a brail, which is a piece of pipe or wood with numerous four-pronged hooks attached. If a hook slides between the valves of a partially opened mussel, the shells clamp shut. After being dragged for several hundred metres, the brail is retrieved and the mussels are stripped off the hooks.

63. Today there is considerable interest in artificially culturing freshwater pearls in this country (Ward 1985, Sitwell 1985). The Tennessee Shell Company is currently conducting experiments on artificial pearl production with American molluscs in a man-made lake in Tennessee. The process of culturing pearls is relatively simple, although a difficult and laborious technique. A piece of mantle tissue is carefully placed in a live mollusc. Next to this is placed a round insert made from a shell usually collected from the Mississippi River drainage. The inserted mantle tissue will grow and cover the nucleus and deposit layers of nacreous material to finally produce a freshwater pearl.

Endangered Mussels

64. Currently the Federal List of Endangered Species includes 28 species of freshwater unionids. *Lampsilis higginsi* and *L. orbiculata*, known from the upper Mississippi River and sites in Tennessee and Arkansas, respectively, are probably the best known of the listed molluscs. However, the list also includes species which are localized and not likely to be encountered in most large-river surveys. An example is *Proptera capax*, now restricted to the St. Francis River in Arkansas, and *Conradilla caelatata*, found only in the Duck River in Tennessee.

65. It appears that some Endangered species are collected in diverse and dense mussel beds. For example, both species of *Lampsilis* have been found in extensive mussel beds, as has the orange-footed pimpleback *Plethobasus cooperianus*. Sites that are suitable for common species provide conditions

for uncommon organisms. In addition, a diverse community of mussels indicates
that many species of fishes inhabit the area. This community model for
mussels is not intended to be used solely for Endangered species; however,
sites that are suitable for a diverse molluscan community have a greater
likelihood of supporting an Endangered or uncommon species.

PART V: HABITAT REQUIREMENTS

66. The following is a discussion of the most important physical
habitat variables (i.e., velocity, particle type, sediment stability) for
thick-shelled mussels. This model is intended primarily for the following
genera: *Quadrula, Amblema, Plectomerus, Megalonaias, Obliquaria*, and
Cbovaria. Information has been taken from the technical literature and
studies conducted by the US Army Engineer Waterways Experiment Station (WES)
for this study. This qualitative information has been converted to 0 to
1 index scores and assembled into a HSI model for thick-shelled mussels.

Variable 1: Velocity (VI)

67. For most invertebrates, current velocity is one of the most impor-
tant parameters and influences food availability, water quality, substrate
composition, as well as amounts and type of in-stream cover (Matteson 1955,
Ciborowski 1982, Shelford 1913). Because mussels are essentially nonmotile,
water currents are necessary to bring in food and disperse sperm and
glochidia. In addition, currents in rivers affect feeding and movement of
fishes, which can influence mussel distribution. The majority of the thick-
shelled mussels are found where water velocities range from 0.15 to 0.46 m/sec
(Buchanan 1980; unpublished information*). Above 0.60 m/sec, the bottom is
usually scoured and unsuitable for unionids.

68. The shells of many mussels exhibit various shapes which enable them
to resist being dislodged by high-velocity water. Shells are truncate,
spined, pustulose, or ridged. The diagonal ridges in *A. plicata, M. gigantea*
(=*gigantea*), and *Plectomerus dombeyana* provide stability, help orient the
mussel in currents, and position the mantle openings in an upright and exposed
position (Clarke 1982, Matteson 1955).

69. The shape of the shell in many freshwater unionids is influenced by
the physical characteristics of its habitat (Ball 1922). Clams from high-
velocity, shallow-water habitats can be compressed and elongate, while
individuals from lentic sites can be more inflated. Clarke (1982) described

---

44

distinctive ecomorphs for *Amblema*, *Pleurobema*, *Fusconaia*, and *Quadrula* in flowing versus nonflowing water.

Variable 2: Particle Type (V2)

70. Substrate composition rather than water quality is probably one of the main determinants of mussel distribution (Arthur and Horning 1969, Fuller 1974) since they are usually embedded in the bottom from one half to three quarters of their body size. Substrate types can probably be categorized into three major types: slab rock, cobble, and gravel; gravel and sand; and mud or silt mixed with sand. Preferred substrate for unionid molluscs is a stable mixture of sand, gravel, and mud (Headlee and Simonton 1906). A firm but penetrable substrate protects mussels from the erosive action of high-velocity water. If mussels cannot dig into the bottom, then large cobbles and rocks can protect them from adverse conditions to some extent. Bedrock and slab rock are not suitable because the mussels cannot move about or anchor easily. If the bottom is too soft, then the mussels sink below the surface and are unable to orient properly (Dawley 1947, Coker et al. 1921).

Variable 3: Sediment Stability (V3)

71. Substrate in a high-quality mussel bed is "armored," a term which refers to firm, well-packed sand and gravel. Diverse and dense mussel communities are never found where the substrate is unstable. If water velocities are in excess of 0.60 cm/sec, gravel and sand will erode, making the site unsuitable for bivalves. In the Missouri River, there are no mussels for 100 km or more above the confluence with the Mississippi River. This is partially the result of the rapidly shifting substrate in this section of the river (Coker et al. 1921).

Variable 4: Deposited Sediment Retained Annually (V4)

72. Sites where sedimentation occurs frequently are easily recognized. However, it may be difficult to identify sites where deposition occurs rarely. The mollusc community at these sites could be dominated by young clams such as small to mid-sized *Quadrula* or juvenile unionids. Biotic and abiotic

conditions might be suitable for establishment of bivalves; however, diverse communities of adults do not become established at sites affected by high sediment deposition and retention, or unstable substrate (Variable 3).

Variable 5: Minimum Depth (V5)

73. The distribution of many aquatic animals is known to be influenced by depth, which influences light, temperature, and dissolved oxygen. The increase in pressure is approximately 1 atm for each 10 m of depth, but fresh-water mussels are restricted to shallow water where pressures are insignificant. Freshwater mussels are commonly collected where the depth is less than 10 m (Cvancara 1972). Clarke (1979) indicates that they often occur near the waterline or among shallow beds of emergent aquatic vegetation. In a study of the Paimionjoki River in Finland, the maximum density of *Unio tumidus* was found at 0.5 m (Haukioja and Hakala 1974). In medium- and large-sized rivers, mussels are usually located in narrow strips along the shoreline where depths range from 0.5 to 6 m. Mussels are excluded from sites with high-water velocity and unsuitable substrate. Typically unsuitable sites are in deep water in the main channel; however, it is not depth per se which limits the molluscs in these cases.

74. In a study of the upper Mississippi River in Wisconsin, Duncan and Thiel (1983) reported that mussel densities were approximately 10 times greater in border habitats than in midchannel sites. Presumably, current velocity and substrate characteristics were as important as depth in limiting unionids from midchannel sites. Since mussels are suspension feeders, there is no reason for them to exist exclusively in the photic zone.

75. Mussels are frequently observed exposed to the atmosphere following a rapid decrease in water levels. If they are in contact with moist substrate and have a source of shade for at least part of the day, some thick-shelled species can survive in this state for days or even weeks. The loss of oxygen caused by persistent shell closure must not be confused with low dissolved oxygen concentrations in the river water. Death from exposure to air is probably related more to buildup of metabolites resulting from prolonged shell closure rather than from drying of tissues.

Variable 6: Maximum Sustained Temperature (V6)

76. Starrett (1971) collected bivalves when summer temperatures ranged from 26.2° C to 31.3° C, although temperatures in the 30s are probably harmful (Matteson 1955). Freshwater mussels have been reported to be most active in the early spring at water temperatures in the 20s (Peach 1982). Grier (1926) observed that mantle flap contractions of *Lampsilis ventricosa* increased from 63 to 128 per minute when temperature increased from 14.5° C to 22.5° C. Flowing water helps to protect molluscs from high temperatures and enables them to survive in areas that could overheat because of solar radiation (Coker et al. 1921). Van der Schalie and Van der Schalie (1950) reported that unionids move from shallow to deep water and become dormant with the onset of cool temperatures.

77. Hydropower facilities on large rivers such as the Cumberland release turbulent, nutrient-poor, cold water for a 4- to 6-hr period each day. Below Wolf Creek Dam in the Cumberland River (southern Kentucky), water temperatures do not exceed 20° C in the summer. The once-dense and diverse mussel fauna (Neal and Allen 1964) is now depauperate with only a few live individuals (Miller, Rhodes, and Tippit 1984).

78. Yokley (1972) found that embryo development in *A. confragosa* did not take place until water temperatures had reached 23° C. Zale and Neves (1982) found that spawning times of lampsiline species in Big Moccasin Creek, a third-order stream in southwestern Virginia, took place between 16.4° C and 25.8° C.

Variable 7: Minimum Sustained Dissolved Oxygen (V7)

79. Bivalves have been collected at sites where dissolved oxygen ranges from supersaturation to complete anoxia (Russell-Hunter 1983). Low oxygen concentrations are most prevalent in the summer months when water levels decline, currents are reduced, and temperatures increase. *A. imbecillis*, which inhabits lotic and lentic sites, was reported to survive 10 weeks of 6-mg/ℓ dissolved oxygen with no mortality (Imlay 1971). Ellis (1931) reported that when dissolved oxygen declined to 20 percent saturation or less, adults became inactive, and that juveniles were more sensitive than adults to reduced dissolved oxygen. Like most invertebrates, unionids are more likely to inhabit a

areas where dissolved oxygen is at least 6 mg/ℓ (Fuller 1974). Dissolved oxygen should be stable with low dissolved carbon dioxide at sites suitable for mussels (Coker et al. 1921).

Variable 8: Calcium Hardness (V8)

80. Dissolved calcium is important to bivalves since it is used to produce the calcareous shell. Poorly buffered waters can experience rapid pH fluctuations; these waters are not suitable since shells can erode (Fuller 1974). At a mussel bed in the Big Black River, Mississippi, a low-pH and calcium-poor system, shells of *Megalonaias* and other clams were heavily eroded.* This erosion was the result of low-calcium water and the erosive action of suspended sediments.

81. Boycott (1936) found that most molluscs in Britain occurred in waters with at least 20 mg/ℓ dissolved calcium. In New York State, Clarke and Berg (1959) had limited success finding freshwater mussels where hardness (as calcium carbonate) was less than 47 mg/ℓ. In New York, Harman (1969) found some species (*Elliptio complanata*, *Alasmidonta undulata*, and *Strophitus undulatus*) that tolerated hardness as low as 21 mg/ℓ; however most mussels were collected where calcium concentrations were greater. Miller, Payne and Aldridge (1986) found a diverse and dense mussel community in the Tangipahoa River in Mississippi where divalent calcium was only 2.5 mg/ℓ, although this is considered to be exceptionally low.

---

* Unpublished information, A. C. Miller and B. S. Payne, 1985, Environmental Laboratory, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Model Applicability

82. The HSI model was prepared using a minimum number of variables
needed to define habitat for freshwater mussels. The life requisites liste
in this model are those determined to be the most crucial to development of
high-quality mussel habitats. For the purposes of this model, it is assumed
that there is a direct relationship between habitat quality and the density
and diversity of the potential community, and that this value can be
quantified.

Geographic Area

83. The gravel bar habitats used to prepare this model were located in
the Upper Mississippi, Tombigbee, Ohio, and Cumberland rivers. However, this
model will be applicable to any large river where freshwater unionid mussels
are likely to be found.

River Size

84. The number of species of mussels found at a site is directly
related to size of the water body. Dawley (1947) found that species richness
varied from 3 in streams less than 25 cm wide, to 11 in streams 25-125 cm
wide, and to 16 in water bodies 1.2-2.5 m wide. In large rivers such as the
Upper Mississippi and the middle and lower reaches of the Ohio, it is not
uncommon to find habitats with 25 or more species of unionids. Larger systems
support more species because of the increased diversity of habitat and the
larger densities and taxa of potential host fishes.

85. Data for this model were collected from rivers ranging from 35 m to
1-2 km wide. The actual size of the river is not significant; however, the
model was developed for large rivers that have a potential for gravel sub-
strate, moderate current velocities, and fairly deep water. It is not
intended for use at sites with soft substrates (mud) or for smaller
production sequence.

Barriers

86. Barriers such as natural falls or artificial dams, if impassable to fish, can affect mussel distribution. Danglade (1914) found no mussels in the genus *Quadrula* above the Falls of St. Anthony in the Mississippi River. Wilson and Clark (1912) found only 4 species of mussels in the Cumberland River above Cumberland Falls (one of which may have been planted), while 19 species were taken in the pool immediately below the falls. Keokuk Dam on the Mississippi River eliminated the skipjack herring from the upper reaches of the river and the bivalve *Fusconaia ebena*, which uses only this fish as its host. In the application of this model, the user must be certain that mussels have the ability to reach the site that is being studied.

Season

87. Since most unionids are long lived (20 years or more), this model can be used during any season. It is important to note that critical times for molluscs could occur during high-water conditions in the spring when substrates are eroded, or during times of oxygen depletion in the summer or early fall. However, the results of erosive action of high-velocity water should be observable during any time of the year.

88. Studies conducted for this report indicate that mussel recruitment in large river gravel bars does not take place every year. Often a community appears to be composed of only a few, or perhaps only one, distinctive age class. While more work in this area needs to be done, evidence indicates it may not be unusual for many years to pass before hydrologic conditions are suitable for successful mussel recruitment.

Minimum Habitat Area

89. In flowing water systems, most mussel beds are linear habitats and can range from tens of metres to kilometres in length. For the purposes of this model, a "bed" consists of a group of mussels with clearly defined boundaries and a density of at least one per square metre.

Verification

90. This model is based largely on community and population demographic data obtained from mussels in gravel bars in large rivers. Total unionid densities at these beds ranged from 19 to 167 per square meter (Table 3). At all of these sites one thick-shelled species dominated, usually either *A. plicata, M. nervosa* (=gigantea) or *F. ebena*. The site with the greatest total biomass was on the Big Black River in central Mississippi. At this site, biomass ranged from 31.6 to 56.0 kg/sq m and clearly dominated the invertebrate community (see also Haukioja and Hakala 1974, and Mann 1964).

91. Based upon quantitative collections at historically prominent mussel beds, at least three recruitment patterns were noted (Figure 15). In the upper Mississippi River (at Prairie du Chien, Wis.), *A. plicata* had a

Table 3

Densities and Total Species Collected at High-Quality Mussel
Beds in Large Rivers of the United States

Location	Density No./sq m	Total Species	Samples*
Ohio River Olmsted, Ill.	60	14	24
Tombigbee River Ala.	29	7	11
Cumberland River Nashville, Tenn.	25	11	10
Mississippi River Prairie du Chien, Wis.	167	26	10
Big Black River Bovina, Miss.	120	13	8
Black River Pocahontas, Ark.	19	14	14

* This is the total number of samples collected to make this determination of density and species richness. In most cases these samples were collected from a single subsite; the total number of quantitative samples obtained at each location ranged from 6 to 30. This model has been prepared following analysis of some of the most productive and historically prominent mussel beds in large waterways of this country.
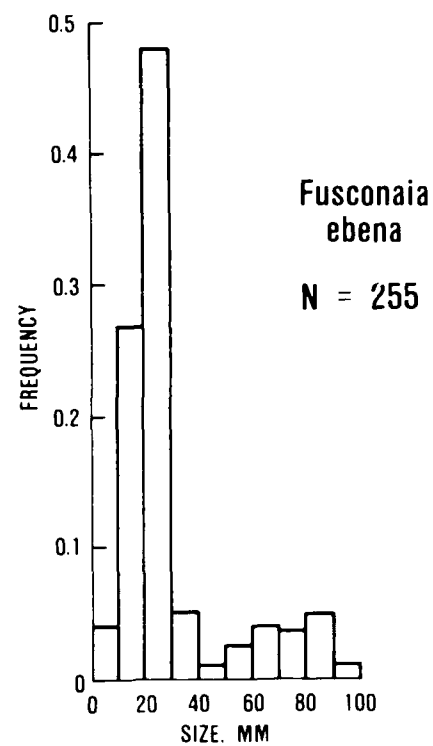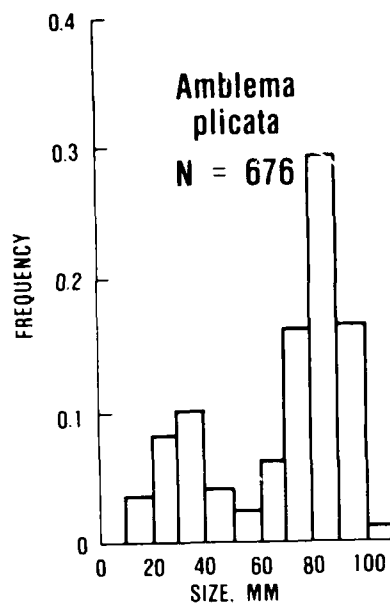
MISSISSIPPI RIVER MILE 635 **OHIO RIVER MILE 967**
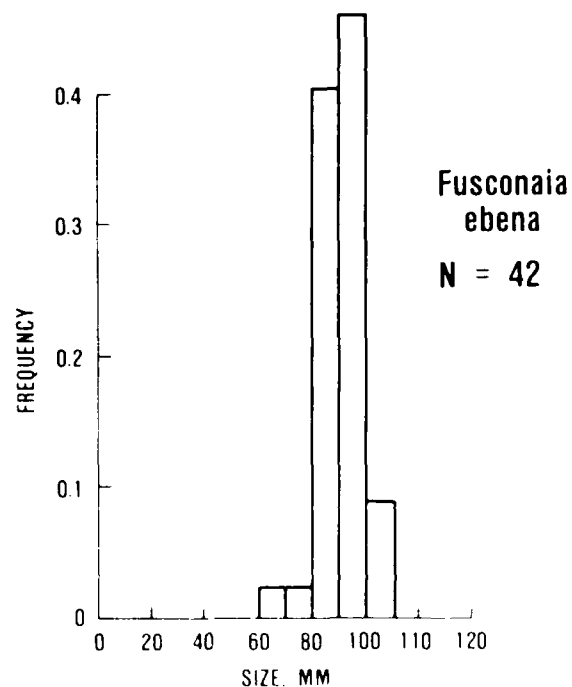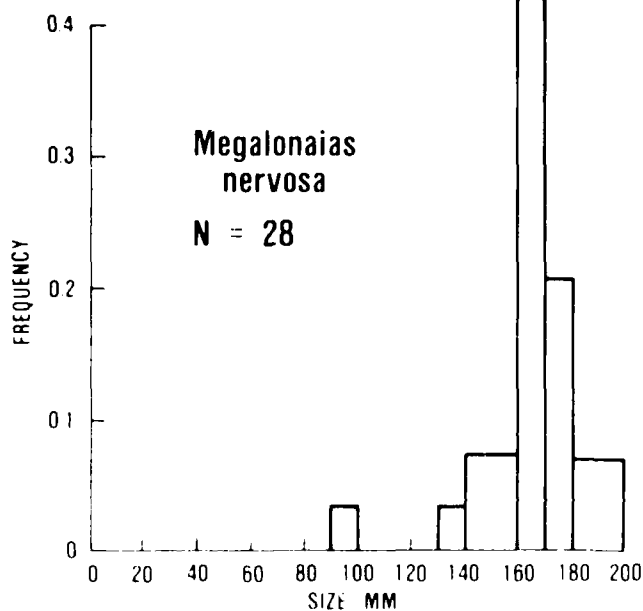
CUMBERLAND RIVER MILE 198 TOMBIGBEE RIVER MILE 263

Figure 15. Shell length-frequency histograms for dominant unionids at historically promient mussel beds in large rivers

bimodal distribution, characteristic of a population with a missing age class. *Fusconaia ebena* in the lower Ohio River exhibited dramatic recruitment; juveniles outnumbered adults by 3:1. At a site near Nashville in the Cumberland River, Tenn., the mollusc community was dominated by adult *M. nervosa* (=gigantea), and no evidence of recent recruitment was noted. The site surveyed on the Cumberland River was characterized by cobble and rock substrate and swift currents, and was not suitable for diverse and dense bivalve communities. The Tombigbee River site showed no evidence of recent unionid recruitment.

Model Description

92. This model uses eight variables to characterize the life requisites of mussels inhabiting gravel bars in large rivers. Six variables (velocity, particle type, sediment stability, deposited sediment retained annually, minimum depth, maximum sustained temperature) pertain to physical conditions, and two variables (minimum sustained dissolved oxygen and calcium hardness) characterize water quality. However, this model assumes no obvious water quality problems such as presence of excessive domestic sewage or industrial effluents. Habitat requirements for adult unionids differ from those of the immature forms or glochidia; this model deals specifically with adult mussels. A demonstration application of the model, using data collected from the Ohio River near Olmsted, Ill., appears in Table 4.

Table 4

Physicochemical Data and HSI Values from Three Historically

Prominent Mussel Beds in Large Rivers

	River					
	Ohio at Olmsted, Ill.		Cumberland at Nashville, Tenn.		Tombigbee at Alabama	
Variable	Value	SI	Value	SI	Value	SI
Velocity, ft/sec	0.2	1.0	0.8	1.0	0.2	1.0
Partical type*	C	1.0	E	0.5	D,E	0.75
Sediment stability, years	5+	1.0	5+	1.0	5+	1.0
Deposited sediment retained annually, cm	0.0	1.0	0.0	1.0	0.0	1.0
Minimum depth, m	8	1.0	5	1.0	5	1.0
Maximum sustained temperature, °C	24	1.0	22	1.0	28	1.0
Minimum sustained dissolved oxygen, % saturation	75	1.0	75	1.0	75	1.0
Calcium hardness, mg/ℓ	30	1.0	25	1.0	29	1.0
Physical conditions		1.0		0.87		0.90
Water quality conditions		1.0		1.00		1.00
HSI		1.0		0.91		0.93

* C = sand and gravel, D = gravel and cobble, E = cobble.

54

SI Graphs for Model Variables

93. SIs for selected variables are given below. Sources of data and assumptions used to develop the SIs are included.

Variable	Source	Assumption
Velocity	Ciborowski (1982) Matteson (1955) Cvancara (1972)	Currents much above 2 ft/sec usually cause severe scouring and erosion of the shell.
Particle type	Harman (1972) Arthur and Horning (1969), Fuller (1974) Cvancara (1972), Dawley (1947) Headlee and Simonton (1906)	The ideal substrate for most mussels is a mixture of sand, gravel, and mud. Extremely fine material does not provide stable conditions and can interfere with burrowing and filter feeding. (A = silt; B = silt and sand; C = sand and gravel; D = gravel and cobble; E = cobble)
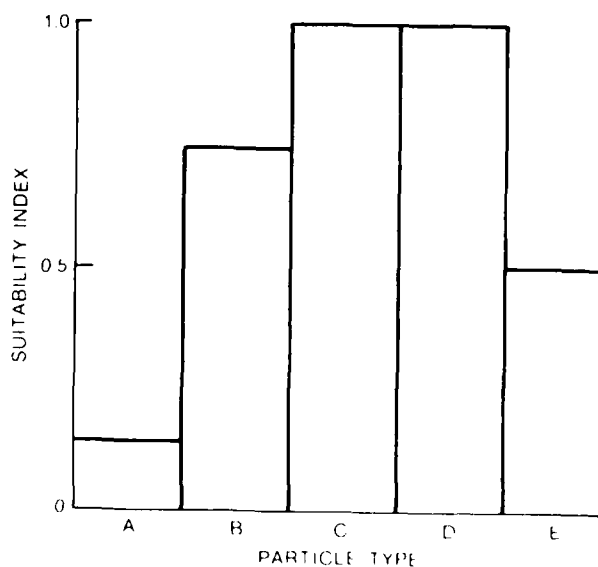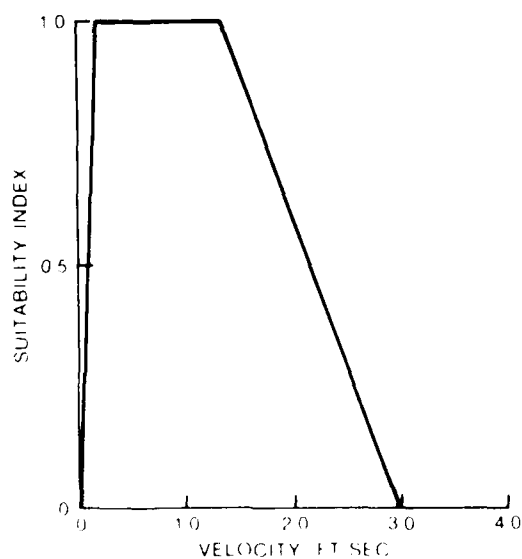
| Variable	Source	Assumption
Sediment stability	Ellis (1931) Coker et al. (1921)	Substrate which shifts or moves will bury adults and juveniles
Deposited sediment retained annually	Ellis (1931) Coker et al. (1921) Harman (1972)	Mussels can tolerate small quantities of deposited sediments. If these are removed by water currents, then the mussels may survive.
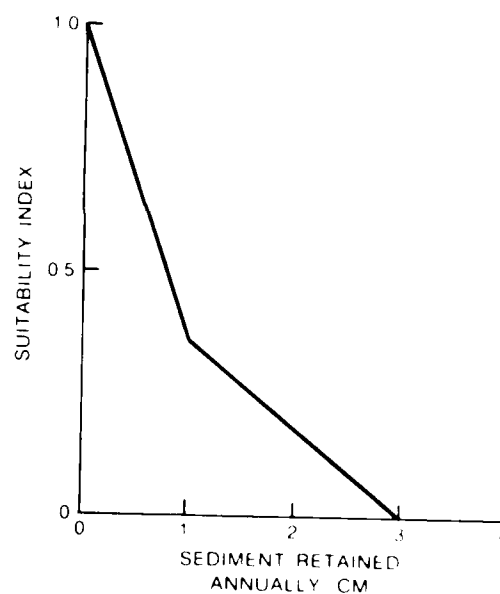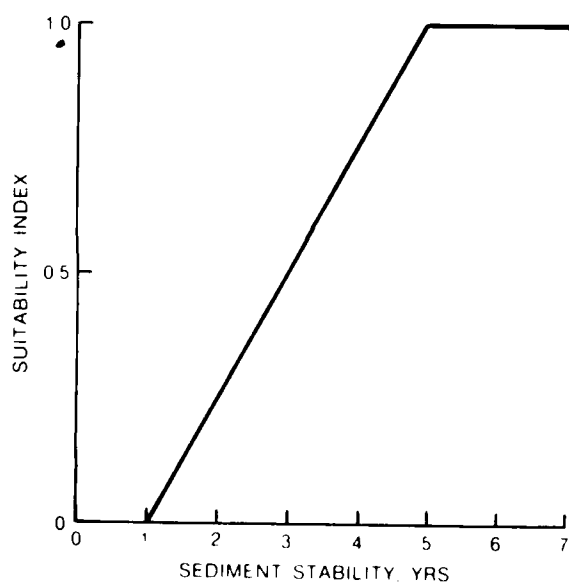
Variable	Source	Assumption
Minimum depth annually	Cvancara 1972 Haukioja and Hakala 1974, Mann 1964 Matteson 1955 Clarke 1979	Past the larval stage, mussels are benthic organisms, usually found in shallow (less than 10 m deep), permanent water.
Maximum sustained temperature	Fuller (1974) Matteson (1955) Starrett (1971) Clarke (1982) Grier (1926)	Mussel communities have been found in water with temperatures above 30° C. However, extended periods of time at these temperatures are detrimental.

Variable	Source	Assumption
Minimum sustained dissolved oxygen	Stokes and Awapara (1968), Russell-Hunter (1983), Imlay (1971) Badman and Chin (1973) Ellis (1931) Coker et al. (1921)	Mussels are able to survive periods of anoxia as well as supersaturation. Dissolved oxygen concentration should be at least 6 mg/ℓ for normal growth and reproduction.
Calcium hardness	Boycott (1936) Clarke and Berg (1959) Harman (1969) Fuller (1974) Wurtz (1962)	Mussel communities are usually found in water with total hardness values. Mussels are found in softer water, although their shells can be eroded. A value of 20 mg/ℓ or more is desirable.

58
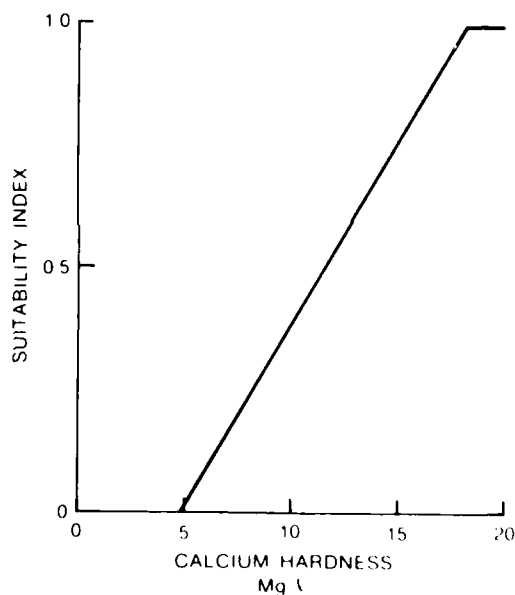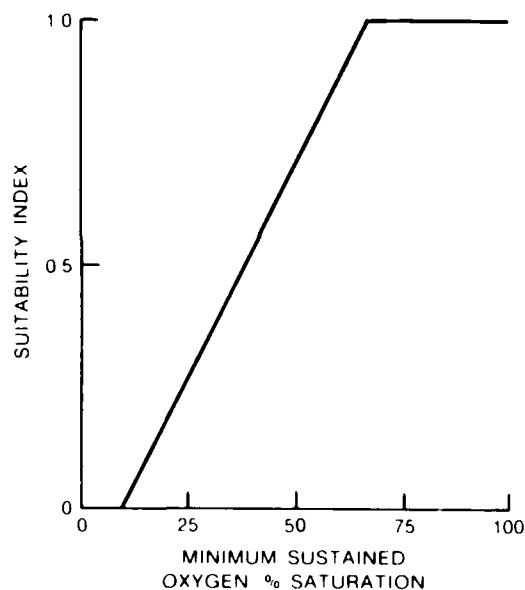
Model Development

94. This model consists of two major components: physical conditions of habitat and water quality.

Physical Conditions (Cp):

$$Cp = \frac{(V1 + 2(V2) + 2(V3) + V4 + V5 + V6)}{8}$$

Water quality conditions (Cwq):

$$Cwq = \frac{(V7 + V8)}{2}$$

HSI determination:

$$HSI = \frac{(2Cp + Cwq)}{3}$$

REFERENCES

Arey, L. B. 1932a. The nutrition of glochidia during metamorphosis: a microscopical study of the sources and manner of utilization of nutritive substances. Journal of Morphology. 53:201-221.

Arey, L. B. 1932b. The formation and structure of the glochidial cyst. Biological Bulletin of Woods Hole. 62:212-221.

Arey, L. B. 1932c. A microscopical study of glochidial immunity. Journal of Morphology. 53:367-379.

Arthur, J. N.; W. B. Horning. 1969. The uses of artificial substrates in pollution surveys. American Midland Naturalist. 82:83-89.

Atkins, D. 1936. On the ciliary mechanisms and interrelationships of lamellibranchs: I. Some new observation on sorting mechanisms in certain lamellibranchs. Quarterly Journal of the Microscopical Society. 79:181-308.

Atkins, D. 1937a. On the ciliary mechanisms and interrelationships of lamellibranchs: II. Sorting devices on the gills. Quarterly Journal of the Microscopical Society. 79:339-373.

Atkins, D. (1937b). On the ciliary mechanisms and interrelationships of lamellibranchs: III. Types of lamellibranch gills and their food currents. Quarterly Journal of the Microscopical Society. 79:375-421.

Atkins, D. 1938. On the ciliary mechanisms and interrelationships of lamellibranchs: VII. Latero-frontal cilia of the gill filaments and their phylogenetic value. Quarterly Journal of the Microscopical Society. 80:345-436.

Atkins, D. 1943. On the ciliary mechanisms and interrelationships of lamellibranchs: VIII. Notes on the gill musculature in Microciliobranchia. Quarterly Journal of the Microscopical Society. 84:187-256.

Badman, D. G.; S. L. Chin. 1973. Metabolic responses of the freshwater bivalve, *Pleurobema coccineum* to anaerobic conditions. Comparative Biochemical Physiology. 44B:27-32.

Baer, J. G. 1952. Ecology of animal parasites. Urbana: Univ. Illinois Press.

Ball, G. H. 1922. Variation in freshwater mussels. Ecology. 3:93-121.

Benjamin, R. B.; Burky, A. J. 1978. Filtration dynamics in the sphaeriid clam, *Musculium partumeium* (Say). Bulletin of the American Malacological Union. 44:60.

Bott, T. L.; Brock, J. R.; Naiman, R. J.; Ovink, R. W.; Peterson, R. C.; C. Stark. 1982. A comparison of benthic community metabolism on four stream systems: a test of the river continuum hypothesis. (In preparation).

Boycott, A. E. 1936. The habits of freshwater Mollusca in Britain. Journal of Animal Ecology. 5:116-186.

Buchanan, A. C. 1980. Mussels (naiades) of the Meramec River Basin, Missouri. 67 p. Aquatic Series, No. 17, Missouri Department of Conservation, Jefferson City, Missouri.

Burch, J. B. 1973. Freshwater Unionacean clams (Mollusca: Pelecypoda) of North America. Biota of Freshwater Ecosystems. Identification Manual No. 11. US Environmental Protection Agency. 176 p.

Burky, A. J. 1983. Physiological ecology of freshwater bivalves. The Mollusca, Vol. 6, pp 281-329. Russell-Hunter, W. D., ed. New York: Academic Press.

Butcher, R. W. 1933. Studies on the ecology of rivers: I. On the distribution of macrophytic vegetation in the rivers of Britain. Journal of Ecology. 21:58-91.

Ciborowski, J. J. 1982. Influence of current velocity, density, and detritus on drift of two mayfly species. Canadian Journal of Zoology. 61:119-125.

Clarke, A. H. 1979. Gastropods as indicators of trophic lake stages. The Nautilus. 94:138-142.

Clarke, A. H. 1982 (May). The recognition of ecophenotypes in Unionidae. Report of freshwater mollusks workshop; May 1982; US Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Clarke, A. H.; C. O. Berg. 1959. The freshwater mussels of central New York with an illustrated key to the species of northeastern North America. Cornell University Agricultural Experiment Station Memoirs. 367:1-79.

Coker, R. E. 1954. Streams, lakes, ponds. Chapel Hill: University North Carolina Press, Chapel Hill.

Coker, R.; Shira, A.; Clark, H.; and Howard, A. 1921. Natural history and propagation of freshwater mussels. Bulletin of the U.S. Bureau of Fisheries, 37:75-182.

Conover, D. G.; Detrick, R. I.; Alexander, J. P.; Burky, A. J. 1981. Comparison of filtration rates as a function of suspended particle concentration in the freshwater sphaeriid clams, *Musculium partumedum* (Sav) and *Musculium lacustre* (Muller). Ohio Journal of Science, Vol 81, Abstr. Suppl., 116.

Cummins, K. W. 1974. Structure and function of stream ecosystems, Bioscience. 24:631-641.

Cummins, K. W. 1975. Macroinvertebrates. Whitton, B. A., ed. River Ecology, Los Angeles: University of California Press.

Cvancara, A. M. 1972. Mussels (Unionidae) of the Red River Valley in North Dakota and Minnesota, USA. Malacologia. 10:57-92.

Danglade, E. 1914. The mussel resources of the Illinois River. Rep US Comm. Fish for 1913, Appendix VI, pp. 1-48. Separately issued in Bureau of Fisheries, Document No. 804, Washington, DC.

Dawley, C. 1947. Distribution of aquatic mollusks in Minnesota. American Midland Naturalist: 38:671-697.

Duncan, R. E.; Thiel, P. A. 1983. A survey of the mussel densities in Pool 10 of the Upper Mississippi River. 14 p. Technical Bulletin No. 139. Department of Natural Resources, Madison, Wisconsin.

Ellis, M. M. 1931. Some factors affecting the replacement of the commercial freshwater mussels. Circulation No. 7, p. 1-10. US Bureau of Fisheries. Washington, DC.

Fryer, G. 1961. The developmental history of *Mutela bourguignati* (Ancev) Bourguignat (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society of London. Series B, 244:259-298.

Fuller, S. H. 1974. Clams and Mussels. Hart and Fuller, ed. Pollution Ecology of Freshwater Invertebrates, New York: Academic Press.

Geraghty, J. J.; D. W. Miller; F. Van Der Leeden; F. L. Troise. 1973. Water Atlas of the United States. Water Information Center Publication, New York.

Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian Niche: bivalve Molluscs of central Canada. Ecology, 52:543-556.

Grier, N. M. 1926. Notes on the naiades of the upper Mississippi drainage: III. On the relation of temperature to the rhythmical contractions of the "mantle flags" in *Lampsilis ventricosa*. The Nautilus, 39:111-114.

Harman, W. N. 1969. The effect of changing pH on the Unionidae. The Nautilus, 83:69-70.

Harman, W. N. 1972. Benthic substrates: Their effect on freshwater Mollusca. Ecology. 53:271-277.

Haukioja, E.; Hakala, T. 1974. Vertical distribution of freshwater mussels in southwestern Finland. Annual Zoological Fennici. 11:127-130.

Hawkes, H. A. 1975. River zonation and classification. B. A. Whitton, ed. Los Angeles: University of California Press.

Headlee, T. J.; Simonton, J. 1906. Ecological notes on the mussels of Wniona Lake. Science. 12:173-179.

Hornbach, D. J., Way, C. M., Wissing, T. E.; Burky, A. J. 1983. Effects of particle concentration and season on the filtration rates of the freshwater clam, *Sphaerium striatinum* Lamarck (Bivalvia: Pisidiidae) and their role in the nutrient dynamics of a woodland stream. Hydrobiologia. 108:83-96.

Hynes, H. B. N. 1970. The ecology of running water. Toronto: University of Toronto Press.

Imlay, M. 1971. Bioassay test with Naiades. Jorgensen and Sharp, ed. Proceedings of a symposium on rare and endangered mollusks of the United States, US Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, pp 38-41. Washington, DC, March 1970.

Jorgensen, C. B. 1975. Comparative physiology of suspension feeding. Annual Review of Physiology 37:57-79.

Kraemer, L. R. 1970. The mantle flap in three species of *Lampsilis* (Peleypoda, Unionidae). Malacologia, 10(1):225-282.

Leopold, et al. 1964. Fluvial Processes in Geomorphology. San Francisco, CA: Freeman.

Livingstone, D. A. 1963. Chemical composition of rivers and lakes. Professional Paper No. 440-G; 64 p. US Geologic Survey.

Mann, K. H. 1964. The pattern of energy flow in the fish and invertebrate fauna of the River Thames. Verh. Int. Verein. Theor. Angew. Limnol. 15:485-495.

Mathis, D. B.; Cobb, S. P.; Sanders, L. G.; Mayoun, A. D.; Bingham, C. Rex. 1981. Aquatic habitat studies on the Lower Mississippi River. Report 3, River Mile 480 to 530. US Army Engineer Waterways Experiment Station, Vicksburg, Miss. 52 pp.

Matteson, M. R. 1955. Studies on the natural history of the Unionidae. American Midland Naturalist, 40:690-723.

Merritt, R. W.; Cummins, K. W. 1984. An introduction to the aquatic insects. Iowa: Kendall/Hunt Publishing Co.

Miller, A. C.; Rhodes, L; Tippit, R. 1984. Changes in the naiad fauna of the Cumberland River below Lake Cumberland in Central Kentucky. The Nautilus. 98(3):107-110.

Miller, A. C.; Payne, B. S.; Aldridge, D. W. 1986. Characterization of a bivalve community in the Tangipahoa River, Mississippi. The Nautilus. 100:18-23.

Minshall, G. W.; Petersen, R. C; Cummins, K. W; Bott, T. L; Sedell, J. R; Cushing, C. L; Vannote, R. L. 1983. Interbiome comparison of ecosystem dynamics. Ecological Monographs. 53:1-25.

Moon, H. D. 1939. Aspects of the ecology of aquatic insect. Transactions of the Society of British Entomologists. 6:39-49.

Morton, J. E. 1958. Molluscs: an introduction to their form and function. 232 pp, Hutchinson University Library, London.

Neal, J. K.; Allen, W. R. 1964. The mussel fauna of the upper Cumberland Basin before its impoundment. Malacologia. 1(3):427-459.

Negus, C. L. 1966. A quantitative study of growth and production unionid mussels in the river Thames at Reading. Journal of Animal Ecology. 35:513-532.

Ortman, A. E. 1909. Unionidae from an Indian garbage heap. The Nautilus. 23:11-15.

Owen, G. 1955. Observations on the stomach and digestive diverticula of the Lamellibranchia: I. The Anisomyaria and Eulamellibranchia. Quarterly Journal of Microbiological Sciences. 96:517-537.

Peach, J. L. 1982. Freshwater mollusks, the commercial approach. Report of freshwater mollusks workshop; May 1982; US Army Engineer Waterways Experiment Station, Vicksburg, Miss.

Reid, G. K.; Wood, R. D. 1976. Ecology of inland waters and estuaries. New York: D. Van Nostrand Co.

Russell-Hunter, W. D. 1979. A life of invertebrates. New York: Macmillan Publishing Co.

Russell-Hunter, W. D., ed. 1983. Ecology. The Mollusca. New York: Academic Press, Harcourt Brace Jovanovich Publishers, New York, 6:281-327.

Shelford, V. E. 1913. Animal communities in temperate America. Bulletin 5 362 p. Geographic Society of Chicago.

Sitwell, N. 1985. The queen of gems - always stunning and now more cultured than ever. Smithsonian. 15(10):41-50.

Stansbery, D. H. 1971a. Rare and endangered mollusks of the Eastern United States. Jorgensen and Sharp, ed. Proceedings of a symposium on rare and endangered mollusks (Naiads) of the United States. US Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, pp 5-18.

Starrett, W. C. 1971. A survey of the mussels of the Illinois River: A polluted stream. Illinois Natural History Survey Bulletin, 30:267-403.

Stokes, T. M.; Awapara, J. 1968. Alanine and succinate as endproducts of glucose degradation in the clam *Rangia cuneata*. Comparative Biochemical Physiology, 25:883-892.

Sweaney, J. L,; Latendresse, J. R. 1982. American freshwater natural pearls. Gemological Institute of America, Los Angeles, p. 177-187.

Trueman, E. R. 1966. Bivalve mollusks: fluid dynamics of burrowing. Science, 152:523-525.

Trueman, E. R. 1968. A comparative account of the burrowing process of species of <u>Mactra</u> and of other bivalves. Proceedings of the Malacological Society of London. 38:139-150.

Van der Schalie, H.; Van der Schalie, A. 1950. The mussels of the Mississippi River. American Midland Naturalist. 44:448-466.

Van der Schalie, H. 1970. Hermaphroditism among North American freshwater mussels. Malacologia. 10:93-112.

Vannote, R. L.; G. W. Minshall; Cummins, K. W.; Sedell, J. R.; Cushing, C. L. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science. 37:130-137.

Ward, Fred. 1985. The pearl. National Geographic. 168(2):192-223.

Westlake, D. A. 1975. Macrophytes. Whitton, B. A., ed. River Ecology. Los Angeles: University of California Press.

Wilson, C. B.; Clark, H. W. 1912. The mussel fauna of the Kankakee basin. Rep. Comm. Fish. for 1911 and Spec. Papers, pp 1-52. Separately issued as US Bureau of Fisheries Document No. 758, Washington, DC.

Winter, T. E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture. 13:1-33.

Wurtz, C. B. 1962. Zinc effects on freshwater mollusks. The Nautilus. 76:56-61.

Yokley, P. 1972. Life history of *Pleurobema cordatum*. Malacologia. 11:351-364.

Yonge, C. M. 1962. On *Etheria elliptica* Lam. and the course of evolution, including assumption of monomyarianism, in the family Etheridae (Bivalvia: Unionacea). Philosophical Transactions of the Royal Society of London, Series B, 244:423-458.

Zale, A. V.; Neves, R. J. 1982. Reproductive biology of four freshwater mussel species (Mollusca: Unionidae). Virginia Freshwater Invertebrate Zoology. 1:17-28.

APPENDIX A: REPORTED FISH HOSTS FOR SELECTED MUSSELS
(from Fuller 1974)

Mussel	Host Fish
1. *Amblema plicata*	shortnose gar
	northern pike
	highfin carpsucker
	channel catfish
	flathead catfish
	white bass
	rock bass
	green sunfish
	pumpkinseed
	warmouth
	bluegill
	largemouth bass
	white crappie
	black crappie
	sauger
2. *Fusconaia ebena*	skipjack herring
3. *Fusconaia flava*	bluegill
	white crappie
	black crappie
4. *Megalonaias nervosa* (= gigantea)	bowfin
	American eel
	gizzard shad
	highfin carpsucker
	black bullhead
	brown bullhead
	channel catfish
	bluegill
	largemouth bass
	black crappie
	white crappie
	sauger
	freshwater drum
	white bass
	flathead catfish
5. *Lampsilis ventricosa*	green sunfish
	sauger
	bluegill

Mussel	Host Fish
6. *Quadrula nodulata*	channel catfish bluegill largemouth bass white crappie flathead catfish
7. *Quadrula pustulosa*	white crappie shovelnose sturgeon channel catfish brown bullhead black bullhead
8. *Quadrula quadrula*	flathead catfish
9. *Elliptio complanata*	yellow perch
10. *Elliptio crassidens*	skipjack herring
11. *Elliptio dilatata*	gizzard shad white crappie black crappie yellow perch flathead catfish
12. *Plethobasus cyphyus*	sauger
13. *Fusconaia cordatum*	rosefin shiner bluegill
14. *Anodonta confragosa*	American eel gizzard shad white crappie freshwater drum rock bass
15. *Lasmigona complanata*	European carp green sunfish largemouth bass white crappie
16. *Lasmigona costata*	European carp
17. *Lampsilis ventricosa*	sauger freshwater drum
18. *Lampsilis ovata*	bluegill smallmouth bass largemouth bass white crappie yellow perch sauger

Mussel	Host Fish
19. *Lampsilis radiata luteola*	tadpole madtom white bass rock bass bluegill largemouth bass smallmouth bass white crappie black crappie yellow perch sauger walleye
20. *Lampsilis teres*	shovelnose sturgeon longnose gar shortnose gar green sunfish largemouth bass white crappie black crappie orange spotted sunfish warmouth
21. *Ligumia recta*	American eel bluegill largemouth bass white crappie sauger
22. *Ligumia subrostrata*	green sunfish bluegill largemouth bass
23. *Ellipsaria lineolata*	green sunfish sauger freshwater drum
24. *Proptera alata*	freshwater drum
25. *Proptera laevissima*	white crappie freshwater drum
26. *Proptera purpurata*	freshwater drum
27. *Truncilla donaciformis*	sauger freshwater drum
28. *Truncilla truncata*	sauger freshwater drum

END

DATE FILMED

FEB.

1988